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ENERGY FLOW THROUGH ARCTIC INVERTEBRATES

AT TRUELOVE LOWLAND, DEVON ISLAND, N.W.T., 75°40'N 84°40'W

by



JAMES KENNETH RYAN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend
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DEDICATION

I dedicate this thesis to Ray Vosciano, a fellow graduate student, and friend, drowned at Friday Harbour while scuba diving for sea urchins, his research animals.

ABSTRACT

Invertebrate ecology was investigated at a coastal arctic lowland, 84°40' W 75°40' N, of Devon Island, between 1970-74, as a component study of an International Biological Program project. The purpose of the study was to measure invertebrate energy flow.

Invertebrate energetics literature was reviewed and criticised. Energy flow was defined to be the quantity of dead (a definition modification) tissue energy produced, plus energy respired, $m^{-2} yr^{-1}$.

The energetics of *Gynaephora groenlandica* and *G. rossii* (Lymantriidae), 2 of about 25 species of Canadian arctic Lepidoptera, were studied as models for measuring energy flow. From 374 collected specimens, parasitization rates and life histories were determined. Caloric values and weights were determined for all stages. Overwintered 1st instar larvae weighed 1.2 mg, and prepupae averaged 879 mg. Observed growth rates determined that the generation time was 10 years, or longer. The standing crop averaged 0.028 mg dry weight m^{-2} . The population structure was reconstructed in cohort units, to calculate energy flow. Yearly assimilation was estimated to be 3.3 cal m^{-2} on raised beaches, and 0.03 cal m^{-2} in meadows. Comparisons suggested that insect herbivory is more significant in temperate than arctic or tropic zones, and that this herbivory normally removes just small amounts of the net primary production.

Standing crop numbers and biomass of all invertebrate taxa were measured at 2 sites. At the meadow, the collected standing crops m^{-2} (arithmetic means, 1972) were dominated by: Enchytraeidae 18,632

(395 mg dry wt.), aquatic Crustacea 19,765 (25.1 mg), Acarina 3231 (13.2 mg), Collembola 8737 (42.6 mg), and Diptera Nematocera 7081 (95.2 mg). At the raised beach, these were: Enchytraeidae 5791 (119.8 mg), Acarina 4899 (28.4 mg), Collembola 18221 (96.8 mg), and all Diptera 271 (15.8 mg). The actual standing crops were estimated from these, using correction factors. Emergence trap studies revealed that the insect emergence in 1972 was 33.2 mg dry weight (908 individuals) m^{-2} of meadow, and 7.6 mg (82 individuals) m^{-2} of raised beach. Results of pitfall trapping and sweep netting indicated that aquatic insect emergence was greater than terrestrial emergence, as was subsequently proven by comparison to terrestrial and aquatic emergence trap results.

A mathematical model was constructed to estimate invertebrate energy flows. Flow rates were determined by season length, in degree days, and respiration rates. Standing crops determined the magnitude of energy flow. Other factors required by the model were weight ranges of growing immatures, fertility and mortality rates, and the relationship between respiration and animal growth. These separate relationships were solved mathematically. The values of several constants were estimated from literature sources.

Truelove invertebrate energy flows were estimated. At the meadow study site, the estimated 1972 energy assimilated m^{-2} by Protozoa was 105 KJ, 30 KJ by enchytraeids, 5.1 KJ by chironomid and sciarid flies, 2.6 KJ by cyclorrhaphous Diptera, 2.3 KJ by all Crustacea, 1.4 KJ by Collembola, and approximately 0.5 KJ by all other invertebrate groups. At the raised beach study site, assimilation was 21.3 KJ by enchytraeids, 6.2 KJ by Collembola, 0.6 KJ by tardigrades,

0.5 KJ by chironomids and sciarids, and approximately 1.5 KJ for all other invertebrates. These values were compared to the primary production rates, and other energy flows, studied in this ecosystem. Most invertebrate energy flow occurred in the soil, through decomposer food chains.

The Truelove Lowland fauna consisted of 241 known invertebrate species. There were 199 arthropod species, of which 158 were insects, belonging to 8 orders. Homoptera, Phthiraptera, Coleoptera, and Trichoptera were poorly represented. The most diverse orders were Collembola (30 species), Lepidoptera (15 species), and Hymenoptera (39 species). The Truelove fauna was compared with those of other Arctic, and Antarctic, areas.

ACKNOWLEDGEMENTS

This thesis bears my name, but is really the product of many. The writing and organization were strongly influenced by my supervisor, Dr. B.S. Heming. He diligently misinterpreted every imprecise statement, and chided every organizational fault, in such detail that the sum of his comments probably equals the total words written here. Dr. George Ball, as my interim supervisor, and department chairman, shared his time and energy selflessly through all my problems. Dr. Brian Hocking, now reincarnated to myriads of diverse organisms, aided me considerably in my studies. I respectfully acknowledge my debt to each of these men. Others in the entomology department also made contributions. I specifically acknowledge Dennis Procter, my co-worker at Devon, and Martin Chance, who criticized my early manuscripts. This was a happy and friendly department, to which I am pleased to have belonged.

Many invertebrate zoologists, particularly entomologists, spent time and effort determining species on my species list. These authorities are named on the list, and I wish to thank each person who provided determinations. Researchers at the Biosystematics Research Institute in Ottawa were particularly helpful, as many offered suggestions about arctic field work, insects to look for, and on my research. Prominent among these were: Mr. J. Anthony Downes, Dr. W.R. Richards, Dr. Monty Wood and Dr. Bill Mason.

Dr. Larry Bliss, the Truelove Lowland IBP director, worked fiercely throughout the project. Hard work and honesty were his trademarks, and he stamped these indelibly on every project participant. Without his energies, the final output of this thesis, and the project, would neither be as complete, nor of the same quality.

Working with Dr. Doug Whitfield, an elegantly brilliant scholar, plasma physicist turned biologist, motivated me to try harder, and try again, when I felt I had done my best already. The computer model I present herein was translated into mathematical and computer logic by Doug, and his skilled assistant Ross Goodwin. Dr. Josef Svoboda, a Czechoslovakian refugee imprisoned 10 years for political idealism, was a continual inspiration to my thoughts and energy. Dr. Donald L. Pattie supervised the insect caloric measurements. Dr. James M. Mayo and his graduate students, particularly Toni Hartgerink, shared their equipment and knowledge for my measurements of insect CO_2 outputs. Dr. Gerard Courtin provided meteorological data. Many others on the project contributed ideas and energy to this undertaking. To be thrust into isolation in the bleak Siberia of Truelove Lowland, and remain sane and active, required the strong spirits provided by my fellow Devon Islanders. It was a great pleasure to work together with these adventurers.

Dr. Steve MacLean, of the Univ. of Alaska at Fairbanks, criticized and offered helpful suggestions about the ideas expressed in this thesis. Dr. O.W. Heal was instrumental in preparing the Protozoa estimates. Dr. John Whittaker, also from the UK Moor House

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Five persons were paid with grant monies to assist me. The first person was Ken Orich. Colin Hergert worked 2½ years on this project, including 2 seasons at Truelove. He built the emergence traps, and I became his assistant; he sought answers to the project questions as though this was his own research; and he questioned my plans until I clearly explained their relevance. In two summers he took one day off work, and collected the first specimen of *Stentoptilia mengeli*. I hired Lewina Leung on Don Pattie's insistence that she was too good to pass up. Josef Svoboda hired her away from me, and found she was so good that he hired her for life, by marriage. Both took this project personally, transcending paid employee status through commitment and determination. Hal Hamilton and Anne Avramenko credibly finished the soil invertebrate counting. Simple though it appears, the data in Table 10 summarizes 2 years of sorting and counting. My sister, Marybeth Ryan, voluntarily fed my *Pieris rapae* larvae for several weeks. Doreen Rendell carefully typed this thesis, and corrected errors.

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Chapter 1

INTRODUCTION

Energy flow studies are comparatively new to ecology. The energetics approach is ecologically eclectic, and gives the field a needed, cohesive theoretical base (Odum, 1971; Krebs, 1972). It attacks a critical problem in ecology: organization. Enormous amounts of ecological data can be collected, yet never reveal a consistent, clear understanding of an ecosystem and how it functions. Energy is involved in, and basic to, all ecological processes. The energy flow approach allows an ecosystem to be divided into any number of compartments, through which the energy entering and leaving must balance with the outgo and input from other compartments. Divisions of ecology which are fundamentally taxonomic are comparable in energy units, the least common denominator of ecological processes.

My project is one component of an International Biological Program (IBP) study at the Truelove Lowland, 75°40' N 84°40' W, of Devon Island. During 1970-74, a total of 26 IBP research projects (including team efforts) were completed at Truelove, of which 4 treated invertebrates. The research for this study, done in the summers of 1970-72 and a visit in 1973, represents 5.3 of a total of 16 invertebrate research seasons in the field.

The Truelove site is one of 8 comprehensive tundra biome projects. Similar IBP studies in other biomes are largely completed, and energy flow results are being analysed and published.

1.1 The Site

The site is rather distinctive. The northeastern coastline of Devon Island rises abruptly in steep cliffs to 300 m a.s.l. Occasional coastal lowlands, created when the rising land exposed former sea beds (Barr, 1971), lie at the base of these cliffs on the edge of shallow Jones Sound. The Truelove Lowland is one of a series of 4 such interconnected lowlands (Hubert, 1972). It has had a flora similar to that present today for 3000-9500 years (Bliss, 1975). The Lowland was largely to completely snowfree 2 months each year, during which time the sun never set. Ice on Water Lake (see map, Figure 5.A for place names), the largest on the Lowland, did not melt entirely in 2 of 5 field seasons. Each year in August the sea ice broke up, and ice packs drifted out; in October the ocean surface refroze.

There were 96 species of vascular plants (Bliss, 1977a), 182 species of lichens (Richardson, 1977), and 176 species of moss (Vitt, 1977) at Truelove. Eleven plant communities have been recognized on the Lowland, with meadow types dominant, followed by dry zone cushion plant communities (Bliss, 1975). The fauna consisted of 3 species of resident, and 4 species of nomadic mammals, 17 species of breeding or occasionally breeding terrestrial birds (Pattie, 1977), and 241 species of invertebrates (excluding nematodes) (Ryan, 1977a).

Two sites, a meadow and a raised beach (= cushion-plant lichen), were selected for intensive study by the Truelove IBP researchers. A rock outcrop area was added in the third field season, but was surveyed only superficially for invertebrates. Most information in this

thesis, particularly that on energetics, is from the 2 intensive study sites.

1.2 Thesis Objectives

In this thesis I investigate energy flow through terrestrial invertebrates at the Truelove Lowland. This is the first such undertaking made in the Canadian arctic, and is one of a small number of broad-spectrum invertebrate energetic studies being done worldwide. The thesis goals were predetermined by the IBP: These goals are quantification of the energy transformed by invertebrates, of the total energy respired, and of the amount of consumable energy they produce, per meter-square per year ($m^{-2} yr^{-1}$). These energies are computed through a mathematical model developed for this thesis. I also report invertebrate standing crops, which represent potential production energy. Since all major invertebrate taxa of the lowland (except Nematoda; provisionally Protozoa) are included in this study, I inventory the taxa collected. The meaning, and methods of measurement, of energy flow are examined in detail with an insect example, moths of *Gynaephora groenlandica* (Homeyer) and *G. rossii* (Curtis).

Chapter 2

INVERTEBRATE ENERGETICS

The quantity of energy released and transformed by invertebrates is presently being investigated in ecosystems throughout the world. The task is exceedingly complex. In contrast to vertebrates (the "other" group of animal consumers), invertebrates have a tremendous diversity of species and habits, are minute, and occur in enormous numbers. Their body temperatures, and hence respiration and development rates, fluctuate with the external environment. The optimum scientific approach to ecological energetics would be to measure energy flow for each species. This is a comparatively simple task with a single or a few vertebrate species, but is "overwhelmingly laborious" to "presently impossible" with invertebrates (Blackith, 1974; Chernov pers. comm., Huhta and Koskenniemi, 1975). This is subtly acknowledged by authors who report detailed invertebrate population numbers, biomass, and biological parameters, but not energy flows (e.g. Willard, 1973d).

Energy flow through all the invertebrates in any ecosystem cannot be measured with the accuracy presently demanded in other scientific disciplines. This is particularly true of studies done in warm climates. In arctic ecosystems, the invertebrate, and total organismic, species diversities are reduced (Dobzhansky, 1950; Downes, 1964; MacLean, 1975). Primary production, the limiting

variable for secondary production, is drastically less than that in other ecosystems (Odum, 1971). Seasons are short and decisively limited by below 0 C weather. Temperatures above 0 C tend to be stable, i.e. they do not fluctuate widely, or reach incapacitating highs. Each factor which reduces the complexity of measuring energy flow increases the potential accuracy of final measurements. Clearly, the arctic is an optimum climatic zone in which to make energy flow approximations. The Truelove Lowland, with its integrated IBP research effort, particularly its input/output data from the other energy flow studies, is an ideal site for estimating annual invertebrate energy flow.

2.1 Selected Literature Review

The quantity of energy flowing through invertebrates has been investigated only recently. Odum (1968) described 6 major steps in the history of energy flow biology, from food web descriptions by Forbes in 1887, to his own energy flow diagrams. Further historical perspective, specifically on invertebrate energetics, by Englemann (1968) and Paris (1967), reveals that there are comparatively few studies in this field. The first general terrestrial study (Bornebusch, 1930), dealing with forest floor invertebrates, is frequently cited, although it is deficient and has been reanalysed several times (Birch and Clark, 1953; Englemann, 1966; Macfadyen, 1963a; Nielsen, 1951). Trophic-dynamic concepts, fundamentally a description of energy flow processes, and considered to be a major advance in ecological thought, were first discussed by Lindemann in 1942. Lindemann's definition of secondary production was modified

by Odum (1956) to be the "rate of new organic synthesis rather than as rate of consumption." Ecosystem energetic theory is expounded in discussions by Slobodkin (1962) and Golley (1968). (I disagree with statements in each of these, in particular with comments about efficiencies (see Section 4.4.2)). The general ecology textbooks of Odum (1971) and Krebs (1972) strongly emphasize energetics; Krebs in particular contains excellent discussions on animal energy flow.

Three IBP handbooks on terrestrial energy flow (Petrusiewicz and Macfadyen, 1970; Phillipson, 1966, 1971) were written as guides for energetics research. The handbook on methods in soil ecology (No. 18, Phillipson), which is most relevant to this research, was not available until my final field season. The contributing authors describe extraction procedures for soil invertebrates, but refrain from recommending sampling programs for all sites. Uniform procedures would have made the data from different IBP sites more comparable. No practical methods to calculate energy flow are provided in any of these handbooks. This is not so much a fault as a fact, reflecting the present state of the science.

Vertebrates, particularly mammals, have received considerably more attention as secondary consumers than have invertebrates. The monumental work by Brody (1964) on agricultural livestock is the most complete reference available on animal energetics. Continuing work in agriculture (Flatt and Moe, 1968) takes energy flow to biochemical levels. Discussions in these works pertain directly, or in principle, to invertebrate studies. The study on African elephant energetics by Petrides and Swank (1966) (reanalysed in Krebs, 1972)

explains the practical measurement of energy flow in clear, simple terms. It is the model for the study I would like to produce on invertebrates.

Studies on single invertebrate species provide the most detailed and accurate information on energy flow, and indicate in a general way the accuracy limits possible in multi-taxa studies. Early research described energy pathways, and aspects of population growth and metabolism. Careful study of the harvestman *Mitopus morio* (F.) (Phillipson 1960, 1961) revealed adult weights, and consumption and respiration rates; but without knowing the population density, structure, and replacement rates of these animals, their energy flow cannot be calculated. (Phillipson diverted his attention from these measurements to another problem of his day, and produced a microbomb calorimeter for invertebrates (Phillipson, 1964). Caloric values measured in this thesis were determined on a Phillipson apparatus). A complete energy flow study of a population of salt marsh grasshopper, *Orchelimum fidicinium* Rehn and Hebard, was calculated from population figures obtained by sweep net sampling (Smalley, 1960). This technique is inefficient for nymphs, which may plunge to the ground, and is questionably efficient for adults. Total ingestion by *O. fidicinium* was estimated to be $107 \text{ kcal m}^{-2} \text{ yr}^{-1}$, a high value when compared to that of the northern grasslands hopper *Encyrtolophus sordidus* (Scudder), which ingested $15.8 \text{ kcal m}^{-2} \text{ yr}^{-1}$ (Bailey and Riegert, 1973). Another early study, on *Pogonomyrmex badius*, reported $16-48 \text{ kcal m}^{-2} \text{ yr}^{-1}$ total assimilated energy, and 0.09 kcal production (Golley and Gentry, 1964), which means that production in this insect is 0.3% of energy flow. There is a problem

in definition of terms here, which is discussed in Section 2.2.

A later study on *P. occidentalis* (Cresson) (Rogers, Lavigne, Miller, 1972) added confusion by reporting energy flow only on a per colony basis, instead of by $m^{-2} yr^{-1}$. An investigation of the population metabolism of the collembole *Onychiurus procampatus* Gisin (Healey, 1967) represented a technical advance. Unlike the invertebrates mentioned above, these are minute animals, which must be extracted from soil, and which have uncertain feeding habits. Healey determined the respiration (R) of the population $m^{-2} yr^{-1}$. He attempted to carry the significance of respiratory metabolism further by concluding that "R is equivalent to 75-90% of energy flow, so that the solution of R to a large extent solves the (energy flow) equation." I disagree (see Section 4.4.2). These early studies (excluding Bailey and Riegert!) reveal components of energy flow, but provide tenuous or incomplete energy budgets.

Several recent, single species, investigations contain both respiration and tissue production rates $m^{-2} yr^{-1}$. Three are from IBP tundra biome sites (Hodkinson, 1973; Hofsvang, 1973; MacLean, 1973). Energy flow through a population of *E. sordidus* was calculated by use of a model (Bailey and Riegert, 1973), while MacLean used a simpler method; these are among the very few publications which explain how energy flow was calculated. Hodkinson worked on the psyllid *Strophingia ericae* (Curt.), and Hofsvang and MacLean used the crane flies *Tipula excisa* Schum. and *Pedicia hanna* Alex. Wolf spiders are evidently good experimental animals (e.g. Edgar, 1971a; Kessler 1971) as can be seen in the detailed energy budget available for *Pardosa* (*Lycosa*) *lugubris* (Walckenaer) (Edgar, 1971b). Edgar separated growth

from gamete production in this energy budget, a valid distinction frequently not made by other authors. There are many fractional energy budgets in the literature, as for adult mites (Steigen, Solhøy and Gyllenberg, 1975; Webb and Elmes, 1972). Feeding studies (e.g. Carefoot, 1973; Moon and Carefoot, 1972; Schroeder, 1971, 1972, 1973) offer significant potential for constructing energy budgets, but must be translated into field population numbers and biomass.

Studies on groups of invertebrate species give a perspective on energy flow through parts of ecosystems. Soil mites have received considerable attention (Englemann, 1968; Luxton, 1972). They are not major energy releasers, but are almost a universal component of soil faunas. The soil fauna has been treated as a unit, using radioactive tracers to determine feeding rates and trophic structure of the major taxa (Edwards, Reichle, and Crossley, 1970; Kowal and Crossley, 1971; McBrayer and Reichle, 1971). The results are qualitative descriptions of soil processes, essential to understanding energetics, but which do not permit the calculation of energy flows. These investigators concluded that most soil invertebrates are saprovores, and that their activity promotes microbial decomposition processes. The radioisotope approach, used in combination with respiration measurements, offers great promise for energy flow determinations. Huhta and Koskenniemi (1975) examined soil invertebrate populations and respiration rates, and determined population metabolism, but did not measure ingestion rates. Field-layer invertebrate (e.g. spiders, grasshoppers, Lepidoptera, etc.) energy and nutrient dynamics have also received attention (VanHook, 1971).

A sophisticated trophic level perspective has been achieved with phytophagous insects in a forest canopy by use of a mathematical model (Reichle *et al* 1973). In this study, leaf consumption was discussed quantitatively, and expressed as a percentage of net primary production. The conclusions of this forest canopy insect study were not based on actual measurements, so they are "hypothetical," in the same sense as my own energy flow results.

There are few published studies evaluating energy flow through all invertebrates in an ecosystem. The first was by Bornebusch (1930). Van Der Drift (1951) repeated parts of this study in greater detail. Macfadyen (1963a, b) provided an overview of invertebrate community energetics. Odum (1971) summarized his own group efforts, which serve as educated estimates of energy flow. There is a series of articles in Ekol. Polska (1971) on energy flow through the invertebrates in 2 Polish meadows. Many of these are difficult to understand because of bad English, but it appears that the separate energy flows reported do not balance with one another. Within the IBP tundra biome, workers at the Moor House site have summarized invertebrate energy flow data (Heal *et al* 1975) (unfortunately the respiration units are unclear), and a Pt. Barrow summary will be forthcoming (MacLean, pers. comm.). Truelove Lowland energy flow is summarized in Bliss (1975) and in further detail in Ryan (1977b). The Cambridge University Press is publishing a series of IBP synthesis volumes, which should contain more invertebrate energy summaries.

Energy theory is the same for aquatic and terrestrial invertebrates. However, some approaches to aquatic studies add

insight, and more rigorous definition, to energetics principles. Waters (1969) and Allen (1971) explored the relationship between production and biomass, and suggested that production can be estimated by use of some multiple of the population biomass. Allen's growth-survivorship curve is a graphic representation of the meaning of production, and its relationship to the standing crop. Further theory in Edmondson (1968), and especially in Zaika (1973), analysed aspects of equations that I use in my own energy flow model in greater detail than analyses in terrestrial energetics literature.

The rate of organic matter incorporation into fecal pellets by marine herbivores is estimated to exceed the rate of incorporation of organic matter into herbivore tissue, so fecal pellets constitute a major potential food source for marine animals (Johannes and Masako, 1966). Similar opinions on the significance of faeces appear in terrestrial invertebrate literature, but the subject has not been examined in as much detail.

An energy budget constructed for preadults and adults of *Daphnia pulex* Leydig revealed a mean Respiration/tissue Production ratio of 0.48 (Richman, 1958, reanalysed by Slobodkin, 1962). A complete energy budget for *Pyrrhosoma nymphula* (Sulzer), a damselfly which overwinters as an intermediate stage naiad, revealed a total lifespan $R/P = 0.9$ (Lawton, 1971), which means that during active growth in the second summer this R/P was 0.6. These and other aquatic studies on growth efficiencies (Welch, 1968) influenced my estimates of R/P in the Truelove production model. The relationship between temperature and development shown for Cladocera by Bottrell (1975) also aided me in developing the model. The degree days (above 0 C)

required for these 8 species to mature in constant temperatures of 5, 10, 15, and 20 C was 34 ± 17.2 C (S.E.), and the total lifespan was 706 ± 29.4 C (my calculations). Such degree day similarity, at different base temperatures, is a tenet of the model.

Several studies of arctic insects emphasize aspects of energetics related, yet not basic, to this study. Nectar secretion by subarctic tundra flowers at Churchill, Manitoba, yielded 1.54 Kg of sugar ha^{-1} (Hocking, 1953). This sugar is sufficient to maintain the flight energy requirements of large populations of biting flies. This approach to the study of energetics has been expanded to include all arctic flower-visiting insects (Kevan, 1970; Kevan and Kevan, 1970; Kevan, 1973). Emphasizing pollination ecology, Kevan (1972, 1975) explored the effects of floral heliotropism on flower-visiting insects. A report on sun-basking as a thermoregulation mechanism for high arctic butterflies (Kevan and Shorthouse, 1970) is convincingly written, but relies on minimal data. The ability of bumblebees to elevate their body temperatures to well above ambient (Heinrich, 1973) neatly demolishes classical concepts of poikilothermy. This endothermic phenomenon is apparently widespread among insects (e.g. Hanegan and Heath, 1970; but Heinrich (pers. comm.) has challenged inconsistencies in the data of this report). Such temperature regulating mechanisms may affect energy expenditure by cold climate insects, but have not been investigated in this study.

2.2 Concepts and Terms

Energy is the ability to do work. Energy has 2 states, potential and kinetic. The *standing crop* of a group of invertebrates

is their potential energy, and changes in the standing crop are changes in potential energy. Kinetic energy is energy flow. It occurs when potential energy in one form, such as a leaf, is transformed into another form, such as an insect. Transformations are never 100% efficient, so some portion, but never all, of the digested leaf becomes insect tissue. Thus, energy is lost in transformations, and also in maintaining homeostasis within the new animal. Some portion of the leaf remains as leaf fragments, and never becomes part of the animal. The boundaries of energy flow are delimited by that energy entering the system through digestion, and by that leaving. Energy leaves as respiration, motion, heat, tissue, and metabolic waste. Respiration, motion, and heat are measured as respiration, and is energy lost from the animal. Transformed energy remaining -- tissue and metabolic waste -- is production.

Energy flow in this thesis is the total energy (in calories or Joules) assimilated $m^{-2} yr^{-1}$. It is equal to the calories consumed minus calories eliminated (faeces, urine) (Petruscewicz and Macfadyen, 1970). *Assimilation* is the sum of 2 components: production and respiration. *Production* is the total tissue accumulated at the death of an organism (and the products of tissues, such as cast skins, and peritrophic membranes), and hence is that available to the next trophic level (Odum, 1971). In botanical terms, assimilation is equivalent to gross primary production, as production is to net primary production. Viable reproductive tissue represents potential production, as does standing crop biomass. It is not considered produced tissue until it is consumed or dies. *Respiration* energy

is lost from the system.

Definition of energy flow terms is difficult. I contradicted myself above when I stated that metabolic wastes are one form of production energy, and then defined them as unassimilated energy. Molecules of ~~waste products~~, rearranged from their original configurations, become available to another trophic level. Faeces, in contrast, are unassimilated parts of food. There are two dilemmas here: 1) problems of practical measurement, i.e. distinguishing between metabolic and fecal wastes, and 2) metabolic wastes differ from animal tissues. In early IBP literature (Petruscewicz and Macfadyen, 1970), metabolic wastes were considered to be unassimilated energy, and were lumped with faeces. Accordingly, I suppressed my own conclusions and used the IBP definition in this thesis. More recently (SCIBP, 1974), metabolic wastes have been defined to be production by the IBP.

The example above was a simple case. Defining production is markedly more difficult. There are 5 definitions of production in IBP handbook No. 13 (Petruscewicz and Macfadyen, 1970). These definitions give different quantities, and cannot be compared directly. This makes it necessary for each author on production to specify exactly how he defines this term. In the study on *P. badius* by Golley and Gentry (1964), where production was 0.3% of assimilation, it was the change in biomass of the ant colony. This definition, where production is change in biomass plus elimination (death), is given in handbook No. 13, and was recently used by Heal and MacLean (1975). Similarly, Allen (1971) defined production as the total amount of tissue elaborated in the population or community under

study during a given time period.

The biomass, or standing crop, of a population represents potential production, so that changes in biomass are changes in potential production. However, this energy has not entered another trophic level. It can be metabolized before an animal dies, and so become respired energy. What type of production occurs when changes in standing crop biomass, and tissue at death, are added? These 2 quantities are distinctly different, one being potential production and the other being tissue available to another trophic level. The result is confusing theoretically.

Invertebrate production should be expressed in absolute terms, i.e. as tissue remaining at death, thus indicating energy transfer to another trophic level. Objections can be raised to this definition. Tissue at death cannot be measured practically. Further, invertebrate tissue may be consumed by other invertebrates, so that the sum of produced dead tissue does not all transfer to other ecosystem components. Production would be similar by either definition, and errors inherent to practical measurements will obscure the differences. I conclude that Allen's definition of production, with a "time of measurement" qualification (=at death), is the most acceptable because it has ecological significance.

Other terminology differences are common in production studies. "Bioenergetics" and "energy budget" may describe investigations such as this. They also describe studies where results are not expressed $m^{-2} yr^{-1}$, but as energy distributed within a population. An energy budget study may be little more than a caloric analysis of several stages of a species, with no life history study (e.g. Moon and

and Carefoot, 1972; Carefoot, 1973). Feeding studies can be considered to be precursor energy budget studies. Here, terminology also varies by author. The "Efficiency of Conversion of Ingestion" of Waldbauer (1968) is Schroeder's (1972) "Gross Efficiency of Growth," and similarly Waldbauer's "Efficiency of Conversion of Digestion" is Schroeder's "Net Efficiency of Growth." To standardize terminology and definitions in this thesis, I follow Petruscewicz and Macfadyen (1970), and Odum (1971). Where these 2 sources disagree -- on production -- I follow Odum.

Energy flow cannot be measured directly, although species diversity, standing crops, respiration rates of individuals, and biological factors can be. Population respiration can be computed through an accurate knowledge of these parameters. However, population respiration cannot be measured directly in the field. Respiration of soil invertebrates cannot be separated from decomposition and plant respiration; photosynthesis (especially by non-vascular organisms) adds a further complication. Tissue production is the quantity of tissue which dies in a season, and, as such, it also can be estimated but not actually measured. An invertebrate population may have high or low production with the same standing crop. This is because energy flow is a rate reaction, governed by time and temperature. Standing crops may be identical in summer and winter, but during winter the invertebrate production rate at Truelove is immeasurably small.

2.3 Special Problems of Energy Flow Measurement

It is easier to explain energy flow than to measure it. I

have stated that each species should be examined separately, then all individual species' energy budgets summed, to properly assess energy flow for all invertebrates. This approach is logistically impossible within the framework of the IBP project. Each species, and group of species, presents its own peculiar problems. I discuss some of these problems below, for 3 major groups.

2.3.1 Protozoa

Minute size, rapid mortality and natality, and great numbers make Protozoa virtually impossible to work with accurately. Extractions of Protozoa require small (1cc or 1 gram normally) units of soil and are labor intensive, so that minimal numbers of samples can be processed. Currently, there is no method to determine protozoan extraction efficiency, but it is almost certainly low, except perhaps for testate amoebae. Any field study of Protozoa suffers unavoidably from these problems. In a warm climate, a single rainfall can provide conditions suitable for the development of one to several generations. Cold dominated environments, where the speed of biological reactions is retarded and the seasons are short, offer the greatest opportunity for assessing the energetic significance of Protozoa. Heal (1965, 1967) made a significant contribution to protozoan energetics with his study on antarctic Signy Island, although his conclusions have them consuming more than the probable net primary production of the area.

Protozoa are Protista, and need not necessarily be included in a study of Animalia. I undertook a limited examination of them because they would have been otherwise ignored at Truelove.

2.3.2 Soil Dwelling Invertebrates

Soil dwelling invertebrates must be extracted from the soil. There are 2 principal methods used to extract soil animals: mechanical extractions, which physically separate the animals from the soil, and behavioral extractions, where the animals leave the soil by their own movements. Behavioral extraction methods are simpler, and generally more efficient (Edwards and Fletcher, 1971). Some animals will not be able to escape from a soil block, especially those injured during its handling, immobile and quiescent stages (eggs and pupae), and moulting animals. Smaller animals must travel proportionately greater distances to escape. Consequently, soil extractions are not 100% efficient. Correction factors must be determined, for each group of animals, to estimate the actual populations.

Until Nielsen (1952) and O'Connor (1955, 1962) published their extraction techniques for enchytraeids, populations of these animals were estimated to be 5-20% of what they are now generally recognized to be (cf. Barnes, 1968). Because soil dwelling invertebrates are not readily visible, and are frequently minute, erroneous population estimates can be made; these go undetected until extraction efficiencies are achieved. Invertebrate extraction technology is improving, but in this study I was limited to using currently available techniques.

Nematoda, Rotifera, and Tardigrada may become inactive during periods of desiccation. This inactive state is known as cryptobiosis, during which time metabolic activity is drastically reduced

(Crowe and Cooper, 1971). Reactivation from the cryptobiotic state can be quite rapid. Thus, the standing crop extracted may have been inactive in the soil. This possibility must be considered when calculating energy flow through invertebrates having cryptobiotic potential.

Collembola, Acarina, and other soil dwelling Arthropoda are rarely recovered in wet, O'Connor type funnels. They are readily extracted with Tullgren funnels, but are collected most efficiently by the Macfadyen high gradient apparatus (Edwards and Fletcher, 1971). These are behavioral type extractors.

Collembola may be used to illustrate a problem inherent to production measurements of soil invertebrates. A population of uniformly distributed Collembola could exist in 2 possible states. In state 1, at one particular instant early each season, all Collembola eggs would hatch, all the immatures would develop uniformly to adults, these would lay eggs simultaneously, and then die at the end of the season. In this state, progressively fewer numbers, of larger individuals, would be recovered by sequential sampling. Collembola production could be calculated easily. In state 2, individuals would require one season per generation as in state 1, but are born and die randomly. In this state, the same number of individuals, with the same population age structure, would be recovered every time by any sampling program. The number of generations per season could not be determined by sampling. In case 2, soil extractions would give only standing crop information, and no indication of production. The actual population state of invertebrates in the field lies somewhere between these extremes. Any production measurement

technique must apply to both population states in a general ecosystem study.

2.3.3 Pterygote Insecta

Winged insects, having an adult stage which flies from the larval home, indicate production rates by the rate of adult appearance. Adults can be trapped as they emerge and attempt to disperse. The total adult mass emerged during a season can be compared to adult emergence at other areas. The differences in emergence reflect differences in production. This makes them unique among the invertebrates. Adult emergence can be compared to the larval standing crop for an approximate measure of turnover rate.

Endopterygote insects (there are no exopterygotes at Truelove) have an immobile but metabolically active pupal stage. These pupae do not feed, and adults usually do not ingest food other than nectar. Both stages rely on larval energy reserves to maintain their high metabolic activity. When other invertebrates are inactive, or not somehow seeking food, their metabolic rates are usually reduced (e.g. during cryptobiosis, or diapause). These differences in lifestyle must be considered by production measurement methods.

Chapter 3

GYNAEPHORA ENERGETICS

Energy budgets have been constructed for selected species of invertebrates at most IBP tundra sites. Bogatschova (1971) studied *Nematus* sp. (Tenthredinidae) in the southern Jamal, USSR; and at Kevo, Finland, consumption by *Dineura virididorsata* (Tenthredinidae) and *Oporina autumnata* (Geometridae) was measured (Haukioja *et al.*, 1973, Haukioja 1973, 1976). At Moor House, England, *Tipula paludosa* Meigen and *Molophilus ater* Meigen (Tipulidae) were studied by Hadley (1971) and Meats (1975), *Strophingia eridania* (Curt.) (Psyllidae) by Hodgkinson (1973), and several species of Cicadellidae by Whittaker (1965, pers. comm.). A complete energy budget for the carnivore *Pedicia hanna* Alexander (Tipulidae) was constructed at Pt. Barrow, Alaska, by MacLean (1973). In Norway, *Tipula excisa* (Schum.) (Tipulidae) was studied by Hofsvang (1973), while adult *Carabodes labyrinthicus* (Mich.) (Oribatei) mites were examined by Steigen, Solhøy, and Gyllenberg (1975).

This chapter presents an energy study for a group of phytophagous insects at Truelove. The moths examined were found to be representatives of two similar species, *Gynaephora* (=Byrdia) *groenlandica* (Homeyer) and *G. rossii* (Curtis) (Lepidoptera: Lymantriidae). At Truelove individuals of both species were rather uncommon, but they are more abundant elsewhere in the Arctic (Bruggemann, 1958; Curtis, 1835; Gibson, 1922). Downes (1962, 1964, 1965) presented the best

accounts of the 2 species as arctic and alpine insects, and summarized their host plant records and early literature. They are among approximately two dozen species of Lepidoptera found in extreme-cold-dominated North America.

I started the Truelove general invertebrate study with few ideas about how energy flow could be measured. What factors have to be known about a species, and which are not essential, to calculate energy flow? Studies with small invertebrates, and with those feeding on poorly defined substrata, were ruled out because of restrictive Truelove field conditions. Both species of *Gynaephora* could be handled, and observed with comparative ease, because they were large, consumed distinct bites of leaves in measureable amounts, and had discrete, solid excreta. Being the largest invertebrates at Truelove, they were conspicuous on the tundra as woolly larvae and silken cocoons. Therefore, I selected them for special study. This chapter describes the results of the *Gynaephora* investigation. It is also a prelude to the invertebrate energy flow model.

3.1 Distribution and Systematic Problems

The distribution in North America of both species is shown in Figure 1. This map was compiled from 19 published papers and museum records (Ferguson, pers. comm., McGuffin, pers. comm.). All specimens were collected in arctic or alpine environments. They were reared from larvae or cocoons more often than collected as adults.

Kozhanchikov (1950) revised this genus in the USSR, and determined that the Soviet specimens belonged to a new species, which he named *G. lugens*. Soviet specimens had previously been determined

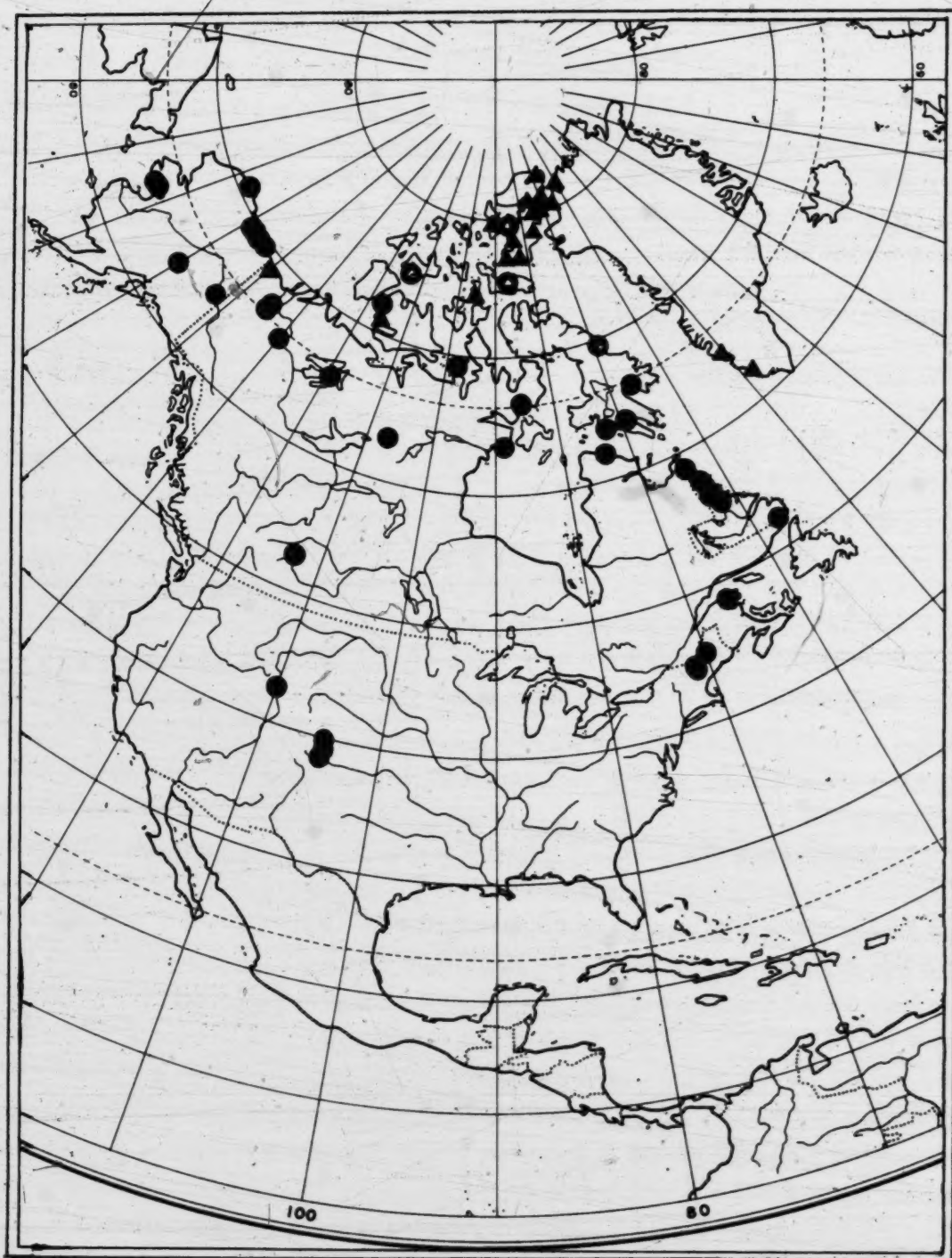


Fig. 1. Distribution of *Gynaephora groenlandica* and *G. rossii* in North America

▲ *Gynaephora groenlandica* ● *G. rossii* ● both species

as *G. rossii* (Aurivillius, 1883; Bryk, 1932; Gaede, 1934). This description creates a disjunct distribution, with *G. rossii* in Japan (Ohyama and Asahina, 1971; Schaeffer, pers. comm.) and North America, and *G. lugens* Koz. in Eurasia. Individuals of *G. lugens* are frequently parasitized by the tachinid fly *Spoggosia gelida* Coq. and by an ichneumonid wasp (Chernov, 1975a), parasites which are common in North American *G. groenlandica* and *G. rossii*. Kozhanchikov did not have access to North American specimens when he published his revision. This indicates the existence of some taxonomic uncertainty so I restricted Figure 1 to North America.

Presently, *Byrdia* is the accepted name for the genus. But Ferguson (pers. comm.), reviewing the family Lymantriidae in North America, states that the correct name for this genus is *Gynaephora*. This revision will appear in The Moths of America North of Mexico.

Individuals of both Truelove species seem identical in food preference and development. They are similar morphologically, and were initially thought to represent one species. The population density of both species is extremely low. Therefore, the data of this study are combined for both species, and referred to as the genus, *Gynaephora*.

3.2 Life History at Truelove

These animals were actively sought and collected from 1970 - 1973 by myself, and by approximately 10 other IBP personnel. Altogether 374 live animals (not including hatchling larvae) and empty cocoons were collected. For each specimen I recorded the following details: location and plant community where found,

developmental stage, weight, and whether parasitized or otherwise unhealthy. Specimens held for observation were kept outdoors in 40 dram, screen-covered, vials.

The mean live weight of all 156 *Gynaephora* larvae collected was 630 mg; the largest larva weighed 1890 mg. The mean live weight of newly hatched larvae was 1.6 mg. As the larvae hatch late in summer, they have limited opportunity to feed. One batch of hatchling larvae, offered continuous food during fall, weighed a mean 1.2 mg live immediately after overwintering. This 1.2 mg is used as the larval starting weight in the synthetic cohort to be discussed later. First stage larvae, carried by wind-blown silk threads, are the dispersal stage.

Seventy-four field-collected cocoons, from which adults emerged, weighed a mean 751 mg live. These cocoons are assumed to have been randomly collected, in terms of their development, and therefore, to be at the midpoint of weight decline for their contained pupae. Cocoon weight just prior to adult emergence was 71% of the maximum larval weight (10 obs.), and adult weight was 56% of this maximum (8 obs.). Mean cocoon weight was 85.5% of the maximum larval weight. Combining these, the maximum live weight of a prepupa is estimated to be 879 mg. This weight is used in the synthetic cohort.

Adult emergence in vials began in June, peaked in late July, and continued through August; emergence times of both species overlapped. No pupae (8 obs.) were observed to survive a winter at Truelove, although adults did emerge from cocoons brought into the laboratory after they would have been killed by frost on Devon. The adult sex

ratio is probably 1/1; e.g. in 1972, 20 male and 25 female adults were reared or collected.

Reproductive capacity was determined by examining female egg loads and eggs deposited. Seven females, at emergence, were found to be 71 ± 2.3 (S.E.)% reproductive tissue, which would be equivalent to 240 ± 24 mature eggs. Females at death still had eggs in their ovaries; thus, they did not deposit the full egg load. Eggs were initially deposited in clumps on the cocoons, and afterwards a few were laid elsewhere. These first clumps (23 obs.) had a mean 139 eggs, while females (16 obs.), held in vials until death, deposited a mean 159 eggs. Eggs from females kept unmated in vials did not hatch. On 19 field collected egg-bearing cocoons, 56% of the eggs failed to hatch. Thus, about half of the eggs laid by *Gynaephora* females were unfertilized, or otherwise not viable. I interpret these data to mean that 160 eggs are deposited per reproducing female, and use this to be the mean reproductive capacity per female in the synthetic cohort. Two females are required to produce one batch of fertile eggs.

Braconid wasps of *Rogas* parasitized larvae of both species, with one wasp emerging from each larva, but in one instance (21 obs.) apparently 2 wasps emerged from one larva. Of 147 *Gynaephora* larvae collected, 15.6% were parasitized by *Rogas* sp.

Tachinid flies of *Spoggosia gelida* Coquillett emerged from cocoons of both *Gynaephora* species, and in 3 instances from larvae of *G. rossii*. Of 118 cocoons examined, 95 *S. gelida* puparia were found, from which 80 adults emerged. The *Gynaephora* cocoons were 17%

parasitized, and parasitized cocoons produced a mean of 4 adult flies. No *Apanteles* sp. wasps, nor *Exorista* sp. tachinid flies, were reared from *Gynaephora*; 3 *Apanteles* sp. are known from Truelove. Dead larvae were not found to be flaccid, as from bacterial or viral death. Fungi (*Aspergillus* sp.) occasionally covered the bodies of dead larvae, but this apparently did not cause the insect death (Kennedy, pers. comm.).

Figure 2 shows the life stages, and parasites, of both *Gynaephora* species.

3.3 Feeding Studies

With feeding studies one can determine the quantity of food consumed by individuals, how much of this remains undigested, and how much is actually assimilated. The assimilated energy can be partitioned into measured growth, and respiration (determined by subtraction). The measured growth indicates, with some qualifications, the growth rates of animals in the field.

3.3.1 Methods

I carried out 3 separate feeding studies with *Gynaephora*, 2 at Truelove and one in an Edmonton laboratory. In the Truelove feeding tests, I report results from 4 larvae in 1971, and 20 in 1972; these tests started with 5, and 62, larvae. The differences are due to pupation, parasitization, death, and non-feeding among the examined larvae. These larvae were maintained in 40 dram screen-capped vials kept outdoors, and were offered selected, weighed green leaves of *Salix arctica* Pall., *Saxifraga oppositifolia* L., and *Dryas integrifolia* M. Vahl. at 4-5 day intervals. Enough leaves were

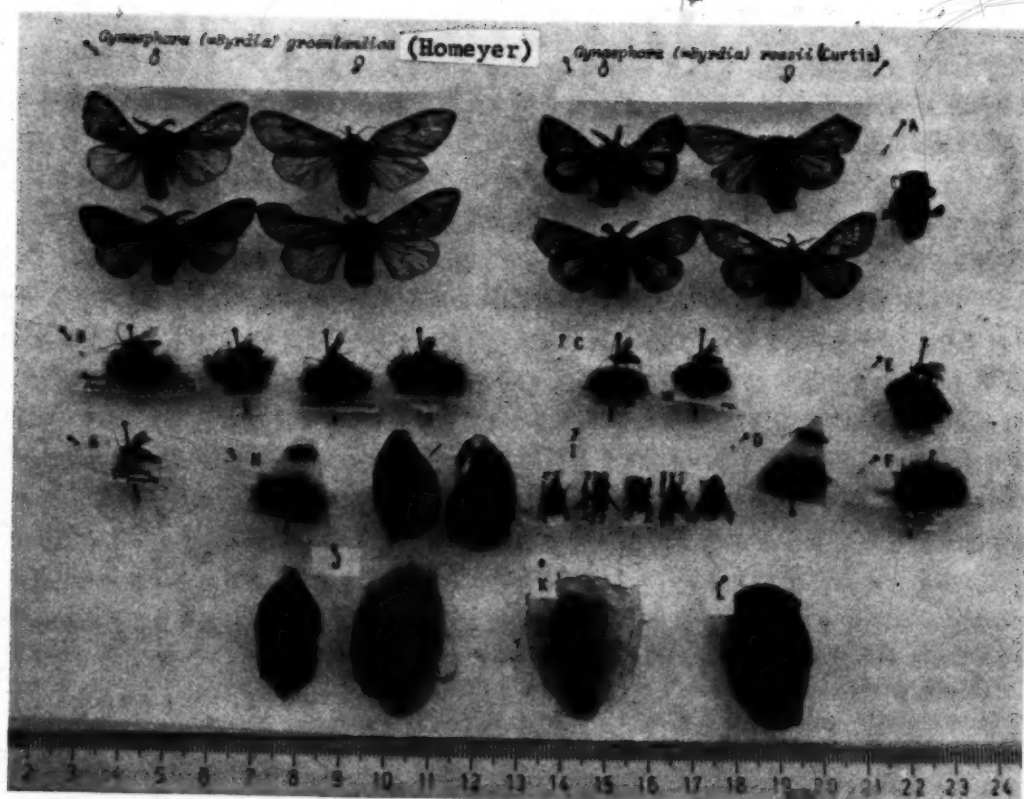


Fig. 2. Stages and parasites of *Gynaephora*, with adults of both species. A. *Gynaephora rossii* female, wings not spread. B. Braconid wasps of *Rogas* sp. on *G. groenlandica* larvae. C. *Rogas* sp. wasps on *G. rossii* larvae. D. *Rogas* sp. wasp on *G. rossii* larva, which also has 14 tachinid eggs. E. *Rogas* sp. wasp on *G. rossii* larva, larva in hibernaculum, parasite emerged early in spring. F. *G. rossii* larva in hibernaculum, died, no parasite emerged. G. Brachypterous specimen of *Rogas* sp. (host sp. undet.). H. Tachinid puparium from *G. groenlandica* larva (only 2 such animals found; adults did not emerge from either). I. Tachinid flies of the species *Spoggosia gelida* Coquillett. J. Light and dark color cocoons (both forms found with each species). K. Opened cocoon to show pupa and larval exuvium (sp. undetermined). L. Eggs laid on cocoon of *G. rossii* (same for both species).

added to each vial to ensure that not all leaves were consumed during the feeding interval. At each food change the uneaten leaves, and faeces produced, were collected and oven-dried, and the larvae weighed. Two sets of controls were maintained for calculating leaf wet/dry weight ratios. One set of leaves, for each leaf type, was weighed and immediately oven-dried, while the other set was kept in empty larval vials and dried when the food was changed. This procedure compensated for weight changes due to leaf metabolism. The live weight of larvae was converted to dry weight by the live/dry weight ratio observed for field collected larvae.

In the laboratory, approximately 150 hatchling *Gynaephora*, held at 23°C, were maintained on *Prunus* sp. and *Salix* sp. until they became 2nd-3rd instars. They were then offered *Rosa acicularis* Lindl. leaves at 3 day intervals.

3.3.2 Results

Results of the 1971 feeding experiment have been published (Ryan, 1972). A detailed computer analysis of the 1972 results appears in Appendix 1. The 1971 Efficiency of Assimilation (E.A.) of mass (= food assimilated/food ingested) of the 4 test larvae was 58%, and the Gross Growth Efficiency (G.Gr.E.) of mass (= larval growth/food ingested) was 10%. Their R/G (= Respiration/Growth, similar to R/Production) was 0.8. In 1972, the E.A. of mass of the 20 test larvae was 24%, and the G.Gr.E. of mass was 8%. Their R/G was 2.0.

Some apparently healthy larvae ceased feeding intermittently, or altogether, and became inactive during these feeding experiments. Larvae maintained without food all summer at Truelove appeared

healthy, with little weight loss, at the end of the summer. Three inactive larvae were held for 9 weeks at 8°C in a temperature cabinet (in Edmonton), during which time their weight declined only 18% from the initial weight. Cessation of feeding had pronounced effects on consumption rates and growth, causing much of the variation in Appendix 1.

The laboratory feeding tests failed. These larvae were successfully reared only to the 2nd or 3rd instar on *Salix* sp. and *Prunus* sp. leaves. Their developmental rates during this initial period are discussed in Section 3.4, on growth.

3.3.3 Discussion

Gynaephora feeding efficiencies are low, as can be seen from the comparisons presented in Table 1. There are several possible explanations for this. Feeding efficiencies for individuals of a single species are known to vary with the food eaten (SooHoo and Fraenkel, 1966). Leaf fiber content is an important factor. Increased fiber content necessitates that more mechanical energy be expended to consume and digest food. Fibrous leaves are usually older and have a lower protein content than young growing leaves (MacArthur, 1972; Schramm, 1972; Verduin, 1972). Leaves of *D. integrifolia*, and *S. oppositifolia*, remain on the parent plants for years, and appear to be thickly fibered. The experimental conditions, including the frequent disturbance of larvae, and the leaves lying flat in vials rather than erect on the host plant, may have reduced consumption. The larvae must continue to respire, however, which lowers their net growth efficiency. Low temperatures appear to have some effect. Soviet arctic tenthredinid larvae, fed *Salix* sp. leaves, had a

Table 1. Comparative growth efficiencies (of mass) of leaf-feeding endopterygote insects

Species	Gross Efficiency (Growth/Ingested)	Net Efficiency (Growth/Assimilated)	Source
<i>Gynaephora</i> 1971	10%	18%	Ryan (1972)
" 1972	4.4%	13%	(14 larvae)
"	10%	27%	(4 larvae with fastest growth)
<i>Mamestra configurata</i> Wlk.	20 - 22.5%	40.5 - 49%	Bailey (1976)
<i>Nematus</i> sp., and			
<i>Phytodecta pallida</i> L.	8 - 10%		Bogatschova (1972)
<i>Pachysphinx modesta</i> (Harris)	14%	46%	Schroeder (1973)
<i>Pieris rapae</i> L.	14%	52%	Ryan (1974)
<i>Platysamia cecropia</i> (L.)	16%	56%	Schroeder (1971)
"	20%	55%	" (1972)
<i>Prodenia eridania</i> (Cramer)	8 - 38%	16 - 57%	SooHoo & Fraenkel (1966)
<i>Pseudaletia unipuncta</i> (Haw.)	17%	48%	Mukerji & Guppy (1970)
9 Lepidoptera species	$\bar{x} = 26\%$ (12 - 34%)	$\bar{x} = 60\%$ (11 - 73%)	Waldbauer (1968)

gross growth efficiency of 9% (Bogatschova, 1971). Arctic host plants, and conditions, have probably contributed to the low efficiencies for these 2 herbivore groups.

3.4 Growth Rates

Growth rates are a controlling factor in energy flow. A species with 10 generations per year will have 10-fold the production, and greater respiration, than a similar species with one generation per year. Food availability is a major determinant of growth rates. Climatic influences, such as the arctic cold, regulate growth rates. Growth can also be negative. The metabolic energy losses of pupae, adults, and diapausing larvae are examples of negative growth. Again, these negative growth rates determine respiratory energy losses, and tissue production rates.

Growth and temperature are related in poikilotherms. Climatic temperatures were measured, and made available for this study (Courtin, pers. comm.). These are compared to *Gynaephora* temperatures, and their relationship is discussed, in this section.

3.4.1 Methods

Growth rates were estimated by using 6 independent techniques.

- 1) In 1972, 6-10 larvae were placed in each of 3 separate walled enclosures of 4-8 m² established on a raised beach. The larvae were weighed periodically, and individual weight fluctuations noted.
- 2) In 1973, 10 larvae were weighed and placed on favorable raised beach sites in emergence traps (Figure 6, Chapter 5) between July 16-31. Nine were recovered and reweighed on September 9.
- 3) Growth rates of the feeding experiment larvae were another measure of development.

These 3 measures of growth were converted to the full season growth rate by multiplying:

$$\frac{(C^{\circ}\text{season total})}{(C^{\circ}\text{obs.})} \cdot (\text{Development, obs.})$$

where C° season total is the accumulated C° days above 0 C, and C° obs. are the accumulated C° days above 0 C while larvae were observed. 4) Approximately 150 hatchling larvae were reared on *Prunus* sp. leaves in the laboratory. The weight increase of the 16 largest larvae surviving was measured after 56 days. These larvae were maintained at a constant 23 C. The development rate at this temperature was converted to Truelove rates by use of the above formula. 5) Collection records from the study site areas indirectly gave a measure of larval development. 6) An estimate of developmental rates was computed from *Gynaephora* respiration rates, from assimilation rates observed in the feeding experiment, and from the mathematical model described in Chapter 4.

Weight losses were measured for larvae, pupae, and adults. Three larvae were weighed, placed without food in an 8 C constant temperature chamber, and reweighed 60 days later. To determine weight loss in the pupal stage, eight animals were weighed, at 4 day intervals, as larvae, then throughout the pupal period, and as newly emerged adults. These were kept outside in screen-capped vials. Thirteen newly emerged adults (6 females, 7 males), after excreting their meconia, were weighed and placed in 2 20x20x20 cm screen cages and were left outside at Truelove. They were given water, but no food. At death, they were oven-dried and weighed, and their lifespans recorded.

To see how climatic temperatures related to *Gynaephora* temperatures, I placed thermocouples outside, and inside, *Gynaephora* larval cast skins and empty cocoons, and measured temperatures under varied weather conditions (see 5.2.1.3 for further discussion).

3.4.2 Results

The growth rates measured and predicted for *Gynaephora* larvae are summarized in Table 2. An additional growth rate indicator (not shown in Table 2) is the collection records from the area of the intensive study sites. The intensity of human activity resulted in more thorough collecting there than elsewhere. Results of this collecting follow: 1970, 12 specimens (3 larvae, 9 cocoons); 1971, 1 larva; 1972, 10 specimens (4 larvae, 6 cocoons). Cocoons are conspicuous and were readily collected, yet none were found here in 1971. The mean weight of collected Truelove larvae was 630 mg, so it is obvious that small larvae were usually overlooked. Prepupae weighed a mean 879 mg (see 3.2). If the larvae of the 1972 pupae grew at the average field-determined rates, they would have weighed between 391-770 mg in 1970. More larvae should have been collected in 1970-71. If these grew at the maximum field-determined rates, in 1970 they would have weighed between 166-382 mg. The maximum rates do not contradict the larval collection records, since such small larvae are likely to be overlooked. From these six growth rate indicators, I conclude that healthy larvae can grow 220% (= 2.2-fold) in a normal ($1285 \times 12^{\circ}\text{C hrs}$) season.

The 3 non-feeding, inactive larvae, held for 60 days at 8 C, metabolized 18.2% of their initial weight. After being frozen at

Table 2. Growth rates of *Gynaephora* larvae adjusted to a 645 °C day
(above 0 C) season

Experiment	Mean Weight Increase	Maximum Weight Increase
walled exclosures	27%, 29%, 50%	50%
screen trap exclosures	14% (9)*	226% (2)*
feeding experiment, 1972	50% (20)	230% (5)
feeding experiment, lab hatchlings	160% (16)	460% (5)
production model: prediction		260%

*Number of larvae observed in brackets

-20 C for 3 months, all pupated when thawed, and an adult emerged from each pupa. These results indicate that *Gynaephora* larvae can diapause, and that this diapausing state curbs metabolic energy losses.

Nine animals spent a mean 38 days within the cocoon before adult emergence. Six of these spent the first 2.2 days as larvae within the cocoons. In the adult lifespan experiments, 6 females lived 13 ± 3.3 (S.E.) days, and 7 males lived 16 ± 2.3 days.

In Section 3.2 I reported initial weights, 1.2 mg. live, and maximum prepupal weights, 879 mg live, of *Gynaephora* larvae. Given the growth rate of 2.2-fold yr^{-1} , the larval development period computes to be 8.6 years. Allowing for retarded growth (bad weather) in one year makes this a 9 year maturation period. Pupation required $\frac{1}{2}$ a season (38 days), mating and oviposition 2 weeks (less than 13-16 days), while egg hatch and larval dispersal occurred before the end of the adult emergence season. Thus, the generation time of *Gynaephora* is 10 years.

Temperatures recorded inside cast larval skins and empty cocoons are given in Appendix 2.

3.4.3 Discussion

I conclude that the yearly increase rate is 220% (slightly more when exuviae are included), and that one *Gynaephora* generation develops in 10 years. One additional growing season beyond the final 879 mg prepupa, at the 2.2-fold rate, would produce a 1934 mg larva; the largest Truelove larva collected was 1890 mg. These data can be interpreted to show slower growth rates, but not faster ones, at Truelove. Rapidly growing larvae are more likely to become adults than slowly developing ones. Slower growth may indicate poor health,

and exposes larvae to greater risks of parasitization, predation, and accidents. Therefore, I am using the maximum rates measured to interpret the growth rates of wild larvae.

Larvae of species in temperate latitudes grow faster than those of *Gynaephora*. For example, *Pieris rapae* L. larvae, reared on cabbage leaves at 23 C, doubled in weight every 3.4 days (Ryan, 1973). Extrapolating to Truelove temperatures, they would have grown 8.2-fold in one season. Life cycles of arctic invertebrates are known to be prolonged due to cold (MacLean, 1975). Downes (1964) estimated the life cycle of *G. groenlandica* to require up to 5 years at Lake Hazen, and later (pers. comm.) suggested 8 years. There are 396 C° days above 0 C at Lake Hazen (2 year mean from Corbet and Danks, 1974) and 273 C° days for the corresponding (my presumption) +2 m meadow measurement at Truelove. Lake Hazen is approximately 1.4-X warmer/longer seasonally than Truelove. By direct conversion of Downes' estimates, the generation time of *Gynaephora* should be 7-11 years at Truelove. I have determined it to be 10 years.

The seasonal temperature I used for the above calculations was 645 C° days above 0 C. This is equivalent to 53.5×12 C° days, a value used later for calculating seasonal respiration. This seasonal temperature is the accumulated degrees between -2 and +2 cm, at the raised beach site, in 1971. This year was the warmest of the 1970-73 period, and -2 cm was warmer than +2 cm. I converted all partial season growth rate measurements to the entire above 0 C season in Table 2. Concerning the feeding experiments, no edible leaves were available in the spring and fall, so the "eating season" was shorter than the above 0 C season. Larvae are active below 0 C, but

I assume that this total activity is negligible compared to that above 0 C. Even if developmental temperature thresholds were known, it would be difficult to determine the relationship of macroclimatic temperatures to those of larval microhabitats. I have used these climatic temperatures because they are precisely determined, and used 0 C as a point of defineable convenience.

Appendix 2 data shows that temperatures inside cast skins and cocoons may be considerably higher than air temperatures, particularly on sunny days. This difference may be most important for pharate pupae, which eclose early each year when there is still much snow on the Lowland, while the days are sunny and clear. Temperatures in the emergence trap were not demonstrably cooler than outside temperatures, so larval growth rates should not have been affected in the traps, nor in the feeding vials.

3.5 Weights and Caloric Values

Weights of all stages of *Gynaephora* were needed for calculating tissue production. Caloric values of these tissues were needed for analysis of the energy aspects of the study. Many of these weights were given in the Life History Section(3.2).

Live individuals were weighed on a Mettler balance, to 0.1 mg. Dry weights were determined on Cahn electro-balances, with maximum sensitivity of ± 0.02 μ g, following 3 days of oven drying at 80 C. A Phillipson micro-bomb calorimeter was used for all caloric determinations. All unburned remains (called residues) were primarily ash, but may have contained organic material.

Table 3 gives the dry weights and caloric values of all stages and tissues of *Gynaephora*, and its parasites. The oven dry weight/live weight ratio of large larvae was 0.225. This is the factor used to convert live larval weights to dry weights in this chapter.

The column showing residue-free caloric values (Table 3) approximates ash-free caloric values. However, unburned organic residues would be the least combustible components of the animal, and have low caloric values. Lipids, and other readily combustible materials, have higher caloric values. Therefore, values in this column can be exaggerations of ash-free caloric values. The number of caloric measurements may be greater than the number of individuals measured, as happens when one individual is halved, and both halves are burned. The caloric value g^{-1} of larvae preserved in 95% ethyl alcohol, 5695 ± 167 , is the same as that of larvae oven-dried immediately after capture ("normal" in the Table), 5682 ± 134 . Their residue-free caloric value standard errors overlap. No detectable reduction in caloric values, as from lipid leaching, resulted from storage in alcohol.

3.6 Respiration Studies

Respiration is energy lost from an animal. It is measurable as O_2 consumed, or CO_2 produced. Procter (1977a) found that hatchling Truelove *Gynaephora* larvae, weighing 0.84 mg live, consumed $0.52 \mu\text{l O}_2 \text{ hr}^{-1} \text{ mg}^{-1}$ at 12 C. At Pt. Barrow, Alaska, Scholander *et al* (1953) found that 450 mg live *G. rossii* larvae consumed $0.19 \mu\text{l O}_2 \text{ hr}^{-1} \text{ mg}^{-1}$ at 12 C. Oxygen consumption may be converted directly to energy metabolized by the oxycaloric equivalent, $3.29 \text{ cal mg}^{-1} \text{ O}_2$ (= 4.7 cal

Table 3. Weights and caloric values for *Gynaephora* and its parasites

Stage	mg Oven Dry Wt Individual ⁻¹ *	No. of Individuals	No. of Measurements	cal g ⁻¹ Oven Dry Wt*	cal g ⁻¹ Residue free Oven Dry Wt*
EGG	0.44	1621	2	6208	7127
LARVA					
1st Instar					
Starved after hatch, died	0.1	184	1	5632	7000
Newly emerged	0.35	276	1	5902	6576
Large, Healthy		12	13	5688±101	6438±137
Larvae preserved in ETOH in field	127.4±50.6	5	6	5695±167	6346±217
Larvae, normal	170.0±37.5	7	7	5682±134	6516±185
Died of Disease?	57.7	3	1	5147	5837
Parasitized					
With 10 tachinid eggs hatched and burrowed in	497.7	1	1	5741	6140
With <i>Rogas</i> parasite	33.6	1	1	5310	--
Larval remains after tachinid emergence	39.1	8	1	5421	6234
Larval exuvium	9.96	37	3	5458	5913
From field	11.65	11	1	5206	5612
From cocoon	9.58	26	2	5697	6198

*Mean ± Standard Error

Table 3 (con't)

Stage	mg Oven Dry Wt Individual ⁻¹	No. of Individuals	No. of Measurements	cal g ⁻¹ Oven Dry Wt	cal g ⁻¹ Residue free Oven Dry Wt
PUPA					
Whole cocoon	196.1±17.7	10	10	5948±102	6776±83
Pupa	178.8±16.2	18	13	5931±74	6787±114
Pupal exuvium	12.3	23	2	4341	5053
Cocoon silk					
Clean	28.8	34	3	4820±67	5343±18
With meconium	56.7±6.9	6	6	4987±82	5944±179
Whole empty cocoon	45.1±4.7	12	12	5260±65	6184±122
ADULT					
Male	64.2±5.8	13	10	6555±107	7394±110
Freshly emerged	74.0±4.5	6	5	6772±113	7313±233
Old	49.5±9.0	7	5	6339±124	7459±95
Female	149.0±14.5	25	17	5823±49	6850±75
Freshly emerged	165.8±14.3	12	13	5899±48	6799±56
Old	79.1	13	3	5615	6987
Reproductive tissues of freshly emerged female	106.4±10.7	7	7	6306±41.4	6954±103
PARASITES					
<i>Rogas</i> sp. (Braconidae)	5.93	3	1	6152	--
<i>Spoggosia gelida</i> Coq. (Tachinidae)					
Pupa					
Live, new	11.7	10	1	5736	6646
Dead, old	7.8	14	1	3266	4122
Empty puparium	1.1	24	1	4805	6155
Adult					
Freshly emerged	12.5	15	1	5842	6780

ml⁻¹). Carbon dioxide production is a less precise metabolic indicator, because the R.Q. (Respiratory Quotient) varies with the substrate metabolized. It can represent a range of metabolic energy (2.56-3.06 cal mg⁻¹ CO₂) (Petreuscewicz and Macfadyen, 1970). The R.Q. for herbivorous insects is normally 0.82 (Bailey and Riegert (1973); (Crescitelli (1935) for *Galleria melonella* pupae; Petruscewicz and Macfadyen (1970); Englemann (1966) reported 0.85).

In this section I analyse my own results, and the oxygen consumption results, to determine *Gynaephora* respiratory energy losses.

3.6.1 Methods

I measured the CO₂ output of *Gynaephora* larvae and pupae on Devon Island in 1971 and 1972, and in the laboratory in Edmonton in 1973. This was done under the supervision of Dr. J.M. Mayo and his graduate students, who analysed net fixation of CO₂ by Truelove plants using Infra Red Gas Analysis (IRGA). I used their IRGA systems.

In field tests I used an MSA analyser, sensitive to ± 2 ppm CO₂. The cuvette temperature varied with ambient temperature, which was not monitored but which was available through daily meteorological records. Respiration was monitored for 15 min intervals. The analyser was regularly calibrated with standard gasses. I made 3 runs with 2 individual larvae in each run in late July -- early August, 1971, and 2 runs with 2 pupae each in July, 1972. All animals were oven-dried and weighed following the runs.

In the laboratory, I used an MSA analyser sensitive to ± 1.0 ppm CO₂, and a Unor analyser sensitive to ± 0.4 ppm CO₂. Larvae were

placed in a respiration cuvette, as shown in Figure 3; this was smaller than the cuvettes used in the field. Temperatures were monitored throughout each run with copper constantan thermocouples. The respiration cuvette was maintained in a Trop-Arctic growth chamber with constant light and controlled temperature (± 1 C). Respiration and temperature were continuously monitored. The analysers were calibrated every 24 hours with standard gasses, and found to be constant. Animals were weighed before and immediately after each run, then oven-dried and weighed.

3.6.2 Results

The results of the 1971 field studies showed that *Gynaephora* larvae having a mean live weight of 506 mg produced an average of $1.82 \text{ mg CO}_2 \text{ hr}^{-1} \text{ g}^{-1}$ dry weight. The approximate air temperature at this time was 6.9 C. These CO_2 production values balanced with those predicted for the 1971 feeding study larvae (Ryan, 1972).

Results of the 1972 pupal respiration measurements were inconsistent due to aggravated temperature fluctuations, and are not reported.

Results of the 1973 laboratory study are given in Figure 4. The average respiration rate of the 2 largest larvae (mean 86.2 mg dry wt), at 6.9 C, was $0.36 \text{ mg CO}_2 \text{ hr}^{-1} \text{ g}^{-1}$ dry weight. The average 1971 field respiration larva dry weight was 113.8 mg. The larval weights are similar, but the CO_2 outputs per gram of larva, $1.82/0.36$, are 5-fold different.

3.6.3 Discussion

There was a large difference between the field-and laboratory-



Fig. 3. *Gynaephora* larvae in cuvette during IRGA CO₂ respiration measurements

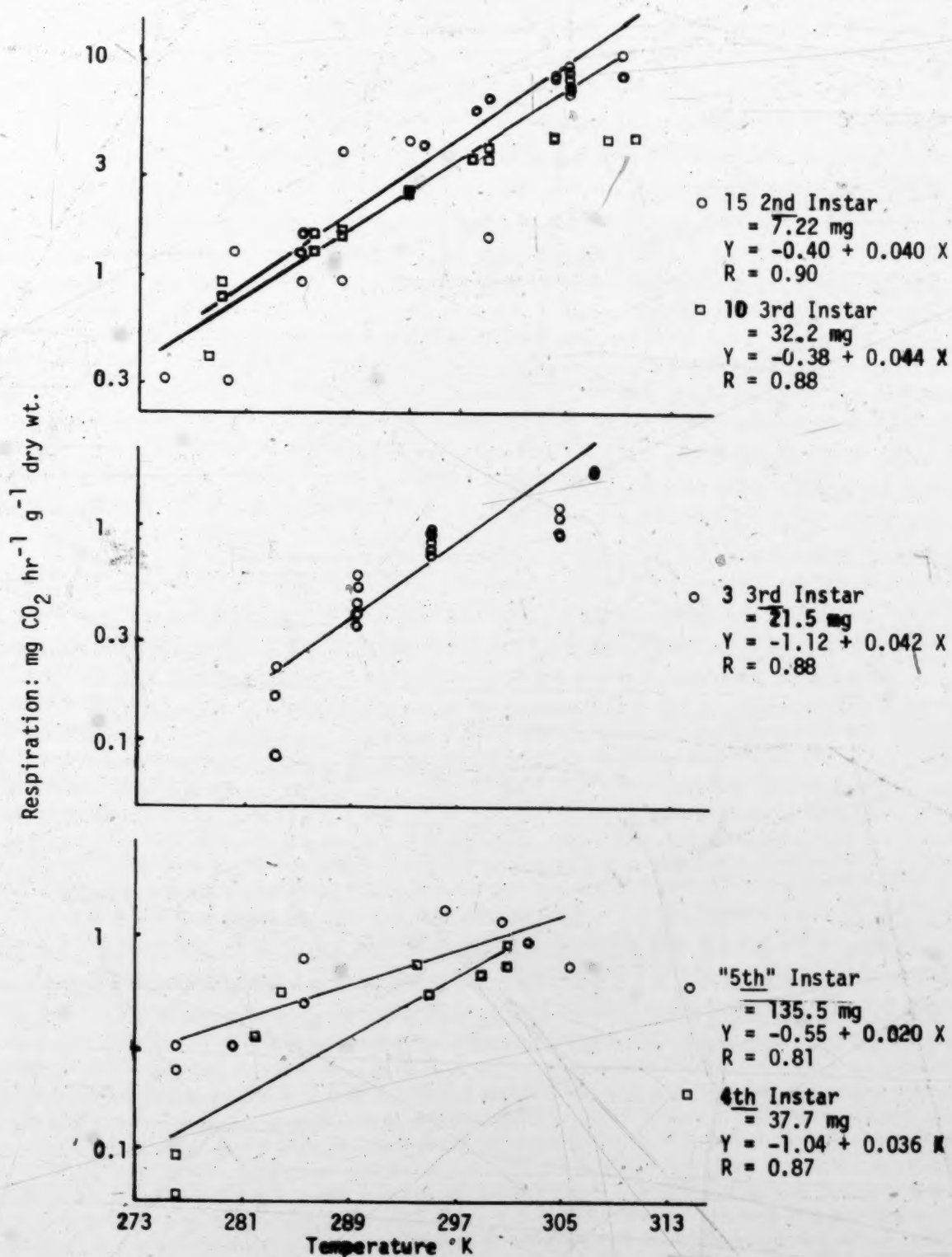


Fig. 4. CO_2 Respiration of *Gynaephora* larvae over a range of temperatures*

*Upper legend refers to upper line on each graph. Weights are mg oven dry weight of all larvae at end of experiment. Respiration is log scale; slope and intercept are log values; these data are converted from Kelvin temperatures.

measured CO_2 respiration results. The respiration rate in the field was higher than that in the laboratory by a several-fold margin. I made a parallel laboratory study with *Pieris rapae* L. larvae, and found that they produced 10-fold more CO_2 than their laboratory *Gynaephora* counterparts. The laboratory *Gynaephora* did not exhibit bursts of activity, as did the field animals. Their low respiration rates probably corresponded to those of inactive (possibly diapausing) larvae observed in the feeding and growth rate experiments. In addition, the field CO_2 production rate was measured under fluctuating temperatures with a comparatively insensitive analyser.

The laboratory study results can be compared to O_2 consumption rates, reported by Procter (1977a), and Scholander *et al* (1953), by use of appropriate conversion factors. As an example, the 3rd instar *Gynaephora* CO_2 respiration rates can be converted into $\mu\text{l O}_2$ consumed hr^{-1} , at 12 C, by using $b = 0.8$, and assuming that the R.Q. = 0.82. The larvae consumed the equivalent of $0.56 \mu\text{l O}_2 \text{ hr}^{-1}$. Scholander *et al*'s *G. rossii* equivalent rate for this larva would be $1.2 \mu\text{l O}_2 \text{ hr}^{-1}$, and Procter's would be $0.94 \mu\text{l O}_2 \text{ hr}^{-1}$.

The *Gynaephora* O_2 consumption rates of Procter (1977a) and Scholander *et al* (1953) are similar. They can be solved simultaneously for the value of b , in $R = aW^b$, giving that $b = 0.77$. This is below the b values usually recorded for insect herbivores (Schroeder and Dunlap, 1970). Scholander *et al* measured *G. rossii* respiration rates over a wide enough range of weights to calculate that its b value was 0.8. Procter's larvae weighed 0.84 mg. Newly hatched *Gynaephora* larvae weighed 1.6 mg, while starved hatchling larvae weighed 0.45 mg at death. Therefore, his larvae were approaching

starvation death. But, they were active throughout the measurement period. Procter's respiration rate was below Scholander *et al*'s, and his larval b value is predicted to be low.

Procter (1977a) measured *Gynaephora* respiration rates, at Truelove, at temperatures of 2, 7, and 12 C. These correspond closely to normal Truelove temperatures. Therefore, I have used his O_2 consumption rate for calculating *Gynaephora* O_2 consumption for all size larvae. These respiration rates are computed by $R = aW^b$, where $b = 0.85$, a is a constant ($a = \frac{0.52}{(0.84)^{0.85}}$), and W is the mean weight of a larva in a specified time interval (this being one growing season in later calculations). Using this higher b value, with Procter's base oxygen consumption rate, results in the prediction that a 450 mg larva respire 0.27 $\mu\text{l mg}^{-1}$. Scholander *et al* (1953) reported 0.19 $\mu\text{l mg}^{-1}$ for this size larva. Thus, Procter's rate, with $b = 0.85$, gives *Gynaephora* larvae the highest respiratory energy loss of the respiration rates available. I do not want to underestimate the quantity of energy respired by *Gynaephora*. By selecting this composite maximum rate, I have maximized the respiration loss.

3. Survivorship in a Cohort

Ideally, a life table should be presented in this section. However, the development of such a table for an insect is a major undertaking. For example, a life table study of the spruce budworm, *Choristoneura fumiferana* Clem., required years of effort, including the full time of 2 researchers, numerous technicians, and their wives (Morris and Miller, 1954). Other life tables cited in this section (Appendix 3) also required extensive manpower resources. At the

Truelove Lowland, *Gynaephora* populations were too low to permit such an undertaking, even if the necessary manpower and funding had been provided. A survivorship curve, which is usually constructed from life table data, is necessary for an energy flow determination to be made. In this section I use data gathered at Truelove, and information from published life tables, to construct a survivorship curve for *Gynaephora*.

Individuals of *Gynaephora* were found in all developmental stages, each year, during this investigation. Thus, the population must consist of overlapping cohorts. The data gathered can be combined, and expressed as information about a synthetic cohort (*sensu* Spinage, 1972). Because a generation spans 10 years, and since the data of this study spans 4 years, the population is considered to be in equilibrium. No measurable population increase or decrease was observed in any year. Equilibrium means that each year a new cohort began to develop, and overlapped identical cohorts developing from previous years.

The mean fecundity of females in the synthetic cohort was found to be 160 eggs. Since half the females produced non-viable eggs, there are at least 2 females in a cohort. Because the sex ratio is equal, there are at least 2 males. Pupae were parasitized at a rate of 17 per 100 by larval *Spoggosia gelida*. This means that 160 hatchling larvae give rise to at least 5 prepupae. Larvae were parasitized at a rate of 15.6 per 100 by larvae of *Rogas* sp., but this rate includes at least 2 larval instars. The Truelove data do not indicate how larval mortality occurred in the cohort between the 160 hatchlings and 5 prepupae.

Exponential mortality, and increase, are the basic assumptions of $e^{r_m t}$ of Andrewartha and Birch (1954). This type of mortality is commonly assumed in invertebrate population growth studies (e.g. Manly, 1974; Wiegert, 1974). Exceptions to exponential mortality are known to occur (e.g. marine oysters, Odum (1971)), but these involve radical changes in habits, habitat, or form of the organism. I examined the mortality rates of phytophagous insects cited by Harcourt (1969) in his review of insect life tables. I plotted the results of these 9 studies, on semi-log paper, as the log of the survivor numbers versus development - rate or stage. The results are given in Appendix 3. The regression value for each, with exponential mortality, was (in order of Appendix 3) $-R = 0.99, 0.99, 0.98, 0.92, 0.96, 0.96, 0.99, 0.96, 0.82, 0.96, 0.97$. This shows that population survivorship is highly correlated to exponential mortality. The lowest correlation occurred with *Tribolium confusum* females, in a laboratory population free of predators, parasites, and pathogens.

I assume that *Gynaephora* larval mortality also occurs exponentially. Time is expressed in degree days, not in solar time; this assumption would be less justifiable if expressed in solar time, because Truelove winters are so long. Until the *Gynaephora* larvae reach a size where parasitism and predation become significant causes of mortality, environmental factors should be the leading causes of death. These operate on larvae of all sizes, and presumably affect each size equally. Predation of larvae by birds is not known to occur at Truelove, but has been observed elsewhere (Bruggemann, 1958; Kozhanchikov, 1950). If mortality is greater in an early instar (e.g. hatchling larvae), then energy flow will be reduced by a small

percentage. The reverse argument, that mortality is highest in later larval instars, is not supported by my observations. If this did occur, then energy flow could be significantly greater than when mortality is exponential. Thus, my assumption of exponential mortality is conservative.

3.8 Standing Crop

The standing crop of *Gynaephora* larvae was estimated from the number of larvae found in 571 m^2 . Most of this count— 500 m^2 —was made using a $\frac{1}{2} \text{ m}^2$ wire frame randomly placed in specific habitats. The 71 m^2 sample is the population found within emergence traps.

The collected standing crop of *Gynaephora* larvae in the 571 m^2 sample was 3 individuals. One larva was found in the 500 m^2 sample, and 2 were found in the 71 m^2 emergence trap sample, on one raised beach. The emergence trap sample was collected over 2 years, so that the 69.8 mg dry collected becomes 34.9 mg yr^{-1} . The average standing crop biomass was $0.206 \text{ mg dry m}^{-2}$.

The *Gynaephora* records show 290 precise collection localities, which can be partitioned into raised beaches, limestone and rock outcrop areas, and meadows. Adjusting the numbers collected by the time spent in these areas gives collection frequency ratios of 13:4:1, respectively, for these land forms. Applying this distribution to the average standing crop collected, the tentative standing crop of raised beaches is 0.45 mg m^{-2} , of limestone and rock outcrops, 0.14 mg m^{-2} , and of meadows 0.035 mg m^{-2} .

The standing crop value is tentative as it is based on only 3 individuals. I believe this value is high. The emergence trap

sample contributed heavily to the standing crop. Other Lepidoptera were distinctly more abundant on the lowland, but only one (an adult) was collected in an emergence trap. Individuals of *Gynaephora* were rare in the field, and these larvae would not be expected to appear in the small number of emergence traps that were set out, whereas other larvae would be. The collection records show that *Gynaephora* were present on many Truelove land forms. My small sample did not indicate the standing crops at these land forms, so I imposed the known distribution over the average standing crop.

3.9 *Gynaephora* Energy Flow

Growth rates, respiration rates, weights and caloric values, feeding efficiency, life history and larval survivorship, and standing crop, of *Gynaephora* have been considered in preceding sections. All these factors are combined in this section to determine the quantity of tissue produced, and the amount of energy lost, by Truelove *Gynaephora* $\text{m}^{-2} \text{yr}^{-1}$.

3.9.1 Energy Flow in a Cohort

The first step in making the final calculations is to compute the energy flow through a synthetic cohort of *Gynaephora*.

3.9.1.1 Results

Exponential mortality during larval development determines the number of individuals dying each year. The weight gain rate determines the mass of a larva at death. For larvae, I assume that the death of each individual occurs at its geometric mean mass for the season. This value, multiplied by the number of larvae

dying that season, gives the amount of produced tissue at death. One pupa dies at mid-stage. One adult dies after emergence, while the other 3 completely exhaust their reserves, and die. Infertile eggs die, so they are produced tissue. Fertile eggs become part of the next generation. Moults produce exuviae, which are another type of tissue production. Table 4 shows these calculations of tissue production in a cohort.

Oxygen consumption in the cohort is calculated in a similar manner. Oxygen consumption for the season is based on the number of individuals calculated to be alive at mid-season, and on their weight at mid-season. Pupal and adult oxygen consumption is determined by weight lost (other than fertile eggs, and tissue produced) from the maximum weight of prepupae. These calculations are shown in Table 5.

Tissue production and O_2 consumption are compared in Table 6. This Table is given in 3 parts. The first shows the amount of each tissue produced, its caloric value, and the caloric amount produced. The second shows O_2 consumed, converted to calories. The third part compares production and O_2 consumption.

3.9.1.2 Discussion

Construction of Tables 4 and 5 required decisions about times of death. In most cases, each decision does not affect total energy flow, but rather puts energy into the produced, or respired, categories. Adult death, for example, could occur earlier than I concluded, but the total cohort energy flow would still be the same. Larval death should not instantaneously interrupt growth, as I assumed. Rather, it may occur over time - an injured animal may ultimately die of starvation or infection. Here again, energy flow

Table 4. Tissue production of *Gynaephora* cohort

Stage or year	No. alive at start of stage	No. died in stage	Mean live wt (mg)/Indiv.	mg Dead Tiss. produced	Exuviae* produced (dry wt)
Egg→larva	160	26	1.4	36	-
2	134	42	1.83	77	-
3	92	28	4.03	113	8.8
4	64	20	8.85	177	11.3
5	44	14	19.4	272	-
6	30	9	42.8	385	30.4
7	21	6	94.1	565	-
8	15	5	157.7	779	40.8
9	10	3	276.4	829	-
10	7	2	608.2	1216	30.8
11 pupa	5	1	713	713	181.1
Adults: unmated	4	1	372; 162**	534	
reproduced		3		395***	
Subtotal				6088	
Dry wt:				1370	303.1
Total				1673 mg dry;	167 mg/yr

*Larval exuvia dry wt was 5.2% live wt of 1st instars, 1.1% of final instar. Exuviae wt produced = (5.2, 4.4, 3.6, 2.8, 2.0, 1.1%)(larvae starting live wt of those which survive that year)

**Infertile eggs

***((mean wt old male + female = 584/2) - (0.1)(584/2)) x (3)

Table 5. Oxygen consumption of *Gynaephora* cohort

Year	$\mu\text{l O}_2$ consumed/ animal/hr	No. animals alive at mid-stage	ml O_2 consumed/animal/season = $(1285 - 12^\circ\text{C hrs}) \times$ $(\text{O}_2 \text{ animal}^{-1} \text{ hr}^{-1})$	Liters O_2 consumed/season = $(\text{No. animals}) \times$ $(\text{O}_2 \text{ animal}^{-1} \text{ season}^{-1})$
1	0.59	148	0.76	0.112
2	0.84	110	1.08	0.119
3	1.4	77	1.80	0.139
4	3.0	53	3.86	0.204
5	5.5	37	7.07	0.261
6	10.5	25	13.5	0.337
7	19	18	24.4	0.439
8	26	12	33.4	0.401
9	46	8.5	59.1	0.502
10	84	6	107.9	0.648
11	82	4.5 pupae 3 adults	48.8* 52.8**	0.220 0.158
				3.540

*approximate life of pupa = 640 - 12 $^\circ\text{C hrs}$ (= 1/2 season)**(386 mg dry wt non-reproductive tissue at emergence) minus (191 mg tissue at death) gives (195 mg tissue metabolized); this is converted to O_2 by 0.85 cc $\text{O}_2 \text{ mg}^{-1}$ tissue (Petrusiewicz and MacFadyen 1970)

Table 6. Caloric relations in one *Gynaephora* cohort

Stage	mg dry wt	cal g ⁻¹	cal produced
all larvae	1000.3	5699	5701
all larval exuviae	122.0	5458	666
all cocoons w/o pupae	181.1	5948	1077
dead pupal remains	160.4	5931	951
all adults	209.0	6032	1261
80 eggs	36.5	6208	226
Total tissue produced:	1709.3		9882

3540 ml O₂ consumed, total
 x 4.7 cal ml⁻¹ O₂ (Petruscewicz and Macfadyen 1970)

16540 calories respired, total

calories in a cohort, total 26422

Ratio: tissue produced/total cal 0.37

Ratio, one larva: respired cal/growth cal
 = (252.9 ml/193 mg + 5.3 mg exuviae) 1.08

is the same, but the P/R changes. Since larval death patterns are not known, I treat death as being instantaneous.

These Tables give my interpretations of event averages. If twice as many larvae become prepupae, total energy flow will be greater: production will be about 1/3 more, and respiration 1/2 more. However, it is unlikely that 2 batches of fertile eggs are required to reproduce a cohort. Such a requirement would cause extinction of the species in periods of low adult abundance. The number of prepupae must be at least 5 to produce one batch of fertile eggs, but should not be as great as 10.

I have assumed that larvae moult 6 times. This was done in response to observations of supernumerary moults in Lepidoptera subjected to cold conditions (Jacobson, 1970), or starvation (Mukerji and Guppy, 1970). *Gynaephora* larvae are exposed to both, and since many collected larvae moulted each spring, I suspect that they had these supernumerary moults. *Lymantria dispar* L. (Lymantriidae) may moult 5-6 times (Goldschmidt, 1934).

Tables 4 and 5 reveal that the bulk of energy flow occurs through large individuals in the cohort. Small and middle size larvae, although numerically abundant, are responsible for only about 25% of the energy flow. Restructuring cohort survival by assuming greater death of dispersing larvae, or by assuming greater survival to prepupae, would increase the energetic significance of larger animals. This suggests that inefficient collection of smaller individuals will not seriously reduce an energy flow determination based on efficient collection of larger individuals.

Table 6 shows that the predicted ratio of larval Respiration/

Growth = 1.08. The 4 fastest growing larvae in the 1972 feeding test had an R/G = 0.87, while the 1971 feeding test R/G was 0.8; the 1972 mean R/G was 2.0. Thus, the predicted R/G fits in-between the independently-observed feeding test R/G's. Larvae can grow only during the "summer", but must respire throughout the season.

3.9.2 Cohort Standing Crop

The measured standing crop can be considered to be some fraction of a synthetic cohort. I make this conversion here.

The total collectable standing crop of larvae and pupae, S_{cc} , in a synthetic cohort is:

$$S_{cc} = \sum_{t=1}^{t_x} N_t W_t$$

where $t_1 \rightarrow t_x$ are the seasons lapsed from larval hatch, to adulthood.

N_t and W_t are respectively the mean numbers, and mean weights, of larvae and pupae alive in the cohort during each "t" season. The mass of synthetic cohort larvae and pupae collectable in one year is found by dividing S_{cc} by the number of years they exist in the cohort, which is 10 at Truelove. The total collectable mass of immature *Gynaephora* in one cohort is 15768 mg live, or 1577 mg yr^{-1} = $355 \text{ mg dry yr}^{-1}$. This value was computed from data in Tables 4 and 5.

The number of synthetic cohorts developing m^{-2} is found by dividing the standing crop actually collected m^{-2} , by the collectable standing crop which would be present when one synthetic cohort develops m^{-2} . The average standing crop biomass was $0.206 \text{ mg dry m}^{-2}$. In synthetic cohorts, this is $0.206/355 = 0.00058$ of a synthetic cohort m^{-2} .

3.9.3 Energy Flow $\text{m}^{-2}\text{yr}^{-1}$

A cohort reproduces itself in 10 years. The Truelove population consists of overlapping cohorts. Therefore, 0.1 of the energy flow in a cohort occurs each year ($= 1285 - 12^\circ\text{C hrs}$). The average standing crop is 0.00058 of a cohort. The average production $\text{m}^{-2}\text{yr}^{-1}$ is $(0.1)(1672.8)(0.00058) = 0.098 \text{ mg}$, or 0.55 cal. Production $\text{m}^{-2}\text{yr}^{-1}$ by habitat, from the habitat distribution baseline, is: raised beaches 0.21 mg ($= 1.2 \text{ cal}$), limestone and rock outcrops 0.066 mg ($= 0.38 \text{ cal}$), and meadows 0.0016 mg ($= 0.0096 \text{ cal}$). Assimilated cal $\text{m}^{-2}\text{yr}^{-1}$ are: raised beaches 3.3 cal, limestone and rock outcrops 1.0 cal, and meadows 0.026 cal.

3.10 Comparisons

These *Gynaephora* energy flow values may be compared to the net primary production on raised beaches and meadows. Svoboda (1977) reported that the above ground net vascular plant production for 1970-72 was $21.6 \text{ g m}^{-2}\text{yr}^{-1}$, of which 14.0 g were woody species, at the raised beach site. These plants were approximately 4500 cal g^{-1} . Assimilation by *Gynaephora* larvae is 0.0052% ($3.3/63000$) of the net above ground vascular plant production, and 0.012% of the net leaf production. The yearly net above ground vascular plant production in meadows was approximately 36 g m^{-2} (Muc, 1977), which, at 4200 cal g^{-1} , is $150000 \text{ cal m}^{-2}$. *Gynaephora* larvae assimilated 0.000017% of this quantity.

The impact of *Gynaephora* larvae on the above ground net primary

production at Truelove may be compared to those of insect herbivores elsewhere. *Gynaephora* larvae assimilated 0.012% of the net leaf production on raised beaches. At the Kevo IBP tundra site, *Dineura virididorsata* (Hymenoptera, Tenthredinidae) assimilated 0.3% of the net leaf production of its host *Betula tortuosa* (computed from Haukioja, 1973, and Haukioja *et al* 1973). *Strophingia ericae* (Homoptera, Psyllidae) assimilated 0.09% of the net foliage production of its host *Calluna vulgaris* at the Moor House IBP site (computed from Hodgkinson, 1973). In a high prairie ecosystem, grasshoppers, which produced a mean $0.23 \text{ mg dry m}^{-2} \text{ yr}^{-1}$ (Riegert and Varley, 1973), assimilated approximately 0.5% of the net foliage production (my conversion, assumed NPP of 600 g m^{-2}); these grasshoppers were the dominant insect herbivores of the site. The consumption of foliage by insect herbivores, at normal population densities, was 2.6% of the net primary production of foliage biomass in a temperate *Liriodendron tulipifera* forest (Reichle *et al* 1973). In the Amazonian tropics, insect herbivory is a comparatively insignificant phenomenon (Fitkau and Klinge, 1973). Insect herbivores, in these ecosystems, normally assimilate minor portions of the net primary production.

Tropical and arctic plants tend to produce perennial leaves while temperate plants are mostly deciduous or annual, and produce leaves with thinner cell walls (MacArthur, 1972). Rapidly growing leaves of temperate plants should be more nutritious (abundant enzymes for growth of leaves themselves; thinner, less fibrous cell walls which are less mechanically obstructive to consumption and

digestion) than those of arctic, or tropical plants. I predict that a general latitudinal pattern exists for herbivore energetics, with herbivorous insects having a proportionately greater role in temperate regions than in the Arctic, or tropical regions.

3.11 Conclusions

The generation time of moths of *Gynaephora groenlandica* (Hom.) and *G. rossii* (Curt.) was estimated to be 10 years at Truelove. Larval gross and net growth efficiencies are among the lowest to be reported for phytophagous insects. Weights and caloric values were measured for all stages. Larvae assimilated $3.3 \text{ cal m}^{-2} \text{ yr}^{-1}$ of leaf tissue on raised beaches, which was 0.005% of the net above-ground vascular plant production. Of this amount, 63% was respired. In meadows, *Gynaephora* larvae assimilated a negligible amount of the net above-ground vascular plant production. *Gynaephora* tissue production was $0.21 \text{ mg (= 1.3 cal) m}^{-2} \text{ yr}^{-1}$ on raised beaches, and $0.0016 \text{ mg (= 0.0096 cal) m}^{-2} \text{ yr}^{-1}$ on meadows. The ratio of Respiration/Growth of larvae was 1.08.

Derivation of the *Gynaephora* energy budget required the following types of data: 1) life history information, 2) weights and caloric values, 3) growth rates, 4) respiration rates, 5) standing crop, and 6) a survivorship curve. Two of these factors, growth rates, and respiration rates, caused energy to flow. Both are responsive to temperature and time, so I expressed this temperature-time relationship in degree days. Life history information, and a survivorship curve, allowed the construction of an interim life table for *Gynaephora*. The assumption that mortality was exponential -

for similar forms, with the same requirements, exposed to the same conditions, with time in degree days - is a conservative one. It permitted energy flow to be estimated for the larval stages. The size of standing crop determined the magnitude of energy flow, when the other 4 factors were known. Weights and caloric values were needed to calculate production.

Chapter 4

ENERGY FLOW MODEL

Energy flow terminology, and special problems in measuring energetics, were discussed in Chapter 2. Any holistic approach to invertebrate energetics must apply, equally, to all the special cases cited there. In Chapter 3, I constructed an energy budget for the moths *Gynaephora groenlandica* and *G. rossii*. Six types of data were necessary to complete this budget. The two factors determining energy flow rate, respiration and growth, were temperature-dependent. The other factors determined magnitude, and direction, of energy flow.

Using this background information, I constructed a model to measure energy flow for all invertebrates. This model allows problems of production and respiration measurements to be considered in a mathematical framework consistent for all invertebrates. In this Chapter, I describe the energy flow model.

4.1 Structuring of Populations by the Model

Since it was impractical to measure energy flow for each species at Truelove, I used higher taxonomic units. In this thesis these units are: Rotifera; Nematoda (treated by Procter, thesis in prep.); Enchytraeidae; Tardigrada; Crustacea: Harpacticoida, Calanoidea plus Cyclopoidea and Ostracoda; Acarina; Araneida; Linyphiidae, Lycosidae; Collembola; Lepidoptera; Diptera:

Mycetophilidae; Tipuloidea, Chironomidae and Sciaridae, Cyclorhapha plus; Hymenoptera: Symphyta, and Apocrita. Protozoa were evaluated with the model, but their energy flow was estimated by use of a simplified analysis. "Plus" means that a small number of other species were included. These taxonomic divisions are units of convenience. They encompass enough physical and ecological similarity, in view of their reduced species diversity, and because of the energetic dominance of each unit by comparatively few species, that reasonable modelling generalizations can be made about each taxon. All parameters assigned to each group are intended to approximate those of the archetype of the group. The archetype is a composite animal, whose attributes are those of the energetically most significant species, with some consideration of less significant species.

Populations within a taxon consist of synthetic cohorts (*sensu* Spinage, 1972), which are subdivisions of the population having mean characteristics of the whole population. A cohort usually contains one fertile female who produces a subsequent identical cohort; it may involve several females contributing to the next identical generation. The populations considered to be in equilibrium in this analysis are the arithmetic means of the 1972 extractions, corrected for extraction efficiency, and the total-season emergence trap catches.

4.2 Basic Equations

Individuals within a synthetic cohort are assumed to behave according to 4 basic equations. The first equation concerns death rates. When cohort individuals live in the same habitat, use the

same resources, and are morphologically similar, the death rate in the cohort is assumed to be exponential with respect to degree day time. The number of individuals, N , present at any time, T , in a synthetic cohort is given by the expression

$$N = N_0 e^{-\alpha T}$$

where N_0 is the initial number of individuals in the cohort and $-\alpha$ is the death rate. If an animal no longer behaves according to the original death rate, such as when an insect larva becomes a prepupa, N becomes N_f . In cases where the adult is similar to the immatures, N_f is 0.5. The cohort is extinguished, and has undergone complete turnover, when less than 0.5 individuals remain alive.

The next basic equation concerns individual respiration rates.

At a constant temperature, respiration varies with weight, and among similar animals this is expressed as

$$R = aW^b$$

where R is respiration, " a " is a constant determined by respiration measurements, W is the weight of an individual, and b is an empirical constant. The values of " a " vary with temperature. Normally b is 0.87 for insects (Schroeder and Dunlap, 1970).

Developing individuals in a cohort gain weight in increments, punctuated by moults. Weight gain is basically a function of body size, which determines food consumption rates, and hence growth rates. The average rate of weight gain is exponential (or at least can be closely approximated by an exponential relationship) in degree day time. The weight, W , of any individual in a cohort at time T is given by

$$W = W_0 e^{\beta T}$$

where W_0 is the initial weight of an individual in the cohort, and β is the growth rate. Where exponential weight gain no longer occurs, such as when an insect larva becomes a prepupa, W becomes W_f . This is the final weight of an animal in the developing part of the cohort, but not the final weight at death.

The last basic equation relates respiration and tissue production, P , in developing animals in a cohort (note that here P is growth, not tissue at death). This relationship is expressed as

$$R = cP$$

where "c" is an empirical constant which means that for every calorie respired, some caloric quantity of tissue is grown.

4.3 Derived Equations, and Other Formulae

The 4 basic equations may be solved simultaneously to determine respiration and production. Only that portion of the synthetic cohort which is actively growing, i.e. immatures, is treated by these equations. Respiration of this portion of the synthetic cohort, R_{sc} , is given by

$$R_{sc} = \frac{\left(\frac{N_0 W_0^b}{a(b\beta - \alpha)} \right) \left(\frac{W_f}{W_0} \right)^b \frac{N_f}{N_0} - 1}$$

Production, P_{sc} , for this same group is

$$P_{sc} = \frac{\left(\frac{N_0 W_0^{\alpha/\beta}}{(1 - \alpha/\beta)} \right) \left(W_f^{1 - \alpha/\beta} - W_0^{1 - \alpha/\beta} \right)}$$

A correction factor of 0.03-0.1, depending on the taxon, is added to the cohort production to estimate tissue loss by moulting. The time required to reach maturity, T_d , is given by

$$T_d = \frac{1}{\beta} \ln \left(\frac{W_f}{W_0} \right)$$

Several equations are important adjuncts to computing energy flow. The mean weight of an immature animal in a synthetic cohort, $\bar{W}_{sc}$, is given by

$$\bar{W}_{sc} = \frac{\left(\frac{W_o}{\alpha} \right) \left[\frac{\left(\frac{W_o}{\alpha} \frac{N_f}{N_o} - 1 \right)}{\left(1 - \frac{N_f}{N_o} \right)} \right]}{(\beta - \alpha)}$$

This equation predicts the mean weight of immatures collected in the field. The mean number of immatures in a cohort, $\bar{N}_{sc \text{ im}}$, is found by

$$\bar{N}_{sc \text{ im}} = \frac{(N_o - N_f)}{\ln(N_o/N_f)}$$

This value divided into the actual field population of immatures m^{-2} gives the number of synthetic cohorts m^{-2} .

The basic operation of the model should be apparent, although an example may make it clearer. An insect, between hatching and becoming a prepupa, gains a measureable amount of weight. Its respiration rate, known for one weight, is calculated for its whole range of weights. The time required to grow to maturity is determined by how much respiration must occur to produce the weight gain observed, given the constant "c" (which is the ratio: Respiration/Production). Some larvae die during development, and this accumulated dead tissue is calculated using the death rate expression.

The adult portion of the synthetic cohort is analysed separately. Where adults use the same resources and habitat as immatures, they follow the same death rate equation used for immatures, although the rate may differ. For these animals, adult respiration, $R_{sc \text{ ad}}$, is

$$R_{sc \text{ ad}} = N \bar{T} a W^b$$

where N is the number of cohort adults and $\bar{T}$ is the mean length of

life of an adult. These adults may gain reproductive tissue weight, which they lose abruptly. They may gain weight allometrically until death, or may become senile and lose weight until starvation death. Unless characteristic weight fluctuations are known, weight in the above expression is W_f , the weight at sexual maturity. Respiration of pupal and adult pterygote insects is computed indirectly from weight lost during both stages. Additionally, adult pterygote respiration is increased by assuming that each adult imbibes $2/3$ of a crop load of nectar (many do not, Kevan, 1970), which is 58% sugar. This is 29% of the exhausted weight of an adult. They metabolize this at an R.Q. = 1.0 (these values are based on Hocking, 1953). Adult pterygote production is the tissue remaining after metabolism.

Results from these equations are converted to respiration and production m^{-2} in 2 steps. The number of synthetic cohorts m^{-2} is found by dividing the seasonal mean population m^{-2} by the mean sampleable number in a synthetic cohort, $\bar{N}_{sc\ im} + \bar{N}_{sc\ ad}$. This sampleable number may be immatures only, e.g. pterygote insect larvae, or adults and immatures, e.g. Collembola. The number of synthetic cohorts developing in one season, Nd_{sc} , is found by dividing the accumulated °C days (above 0 C) in a season, °D, by the °C days required to complete one synthetic cohort, °D_{sc}. Thus

$$Nd_{sc} = °D / °D_{sc}$$

Combining these 2 steps gives the number of cohorts produced m^{-2} in a growing season. This number multiplied by the total synthetic cohort production, and respiration, gives the total energy flow for the taxon.

4.4 Discussion on the Model

The elemental logic of the model, and its basic input values, are considered here.

4.4.1 Time and Temperature Inputs

Time and temperature are interdependent in poikilotherms. In the model, time is expressed as accumulated degree days above 0 C. Respiration and marginal activity may occur below this temperature, but the movement of animals, and food availability, will be restricted by ice. Animal activity increases progressively above 0 C. This increase is mirrored by higher respiration rates.

Meteorological records (Appendix 8.D.II) showed that at -1 cm there was an accumulation of 624°C days above 0 C at the raised beach site, and 313°C days at the meadow. These are the means for the 1971-73 seasons (the 1971 season temperature at -1 cm is extrapolated from adjacent profile temperatures). The yearly mean accumulated degree days are defined as the growing season at each site for the model calculations.

4.4.2 Analysis of the Basic Equations

The model is built upon 4 basic equations. Two of these are straight-forward: respiration, $R = aW^b$, and the relation between respiration and production, $R = cP$. The respiration expression is widely used by physiologists. Respiration rates used in the model are from Scholander *et al* (1953) and particularly from Procter (1977a) measured at this site. The value "a" was calculated from these data

from the expression $R = aW^b$. This "a" value for each invertebrate group was used in the model. Procter measured respiration at 2, 7, and 12 C. With his data, the developmental time calculated was the mean of the 3 temperature based developmental times. Where no arctic respiration measurements were available for a particular group, estimates were substituted from related groups, or from studies of the same group made at temperate latitudes (Protozoa). Respiration was converted to calories by use of the oxycaloric equivalent $4.7 \text{ cal ml}^{-1} \text{ O}_2$ consumed (Petruscewicz and Macfadyen, 1970).

For mammals, "b" is generally accepted to be 0.75 (Brody, 1964, Kleiber, 1961), but for invertebrates the value varies with the observer. Zeuthen (1953) reported a range of 0.63-1.0 for a variety of invertebrates, and Prosser (1973) cited a range of 0.66-1.0 for 27 invertebrate groups, with a majority of values lying between 0.85-0.95. Comita (1968) and Roff (1973) reported that "b" was approximately 0.7 (0.62-0.72) for the Char Lake (200 ml west of Truelove) copepod *Limnocalanus macrurus* Sars. Petruscewicz and Macfadyen (1970) stated that b is "a power of the order of 0.75." Keister and Buck (1974) agreed that "b" is normally a constant, but listed several factors - age, stage, activity, nutritional state, storage material - that can affect its magnitude. Schroeder and Dunlap (1970) presented data to show $b = 0.87$ for phytophagous insects, and explained that without storage tissue this value would be greater. The respiration rate - weight slope of 20 soil dwelling invertebrate species, plotted by Reichle (1968), was 0.85. Throughout this analysis I use $b = 0.87$, which is the approximate median and mean of the above values.

The relationship between respiration and production in immatures, $R/P=c$, is empirical. Consumption and growth rates, and hence production, vary while some minimal level of respiration must always occur if the animal is to remain alive. Thus, the R/P ratio varies upwards from some minimum value. In laboratory feeding tests, high survival rates are thought to indicate proper techniques, and results are given as means of the survivors R/P ratios. Individual R/P variation does not affect survival in a laboratory colony, but may determine survival in a field situation. The mean results of laboratory experiments may not be applicable to field conditions. I use the minimum justifiable values for c , usually 0.5 (cf. Waldbauer, 1968: (Assimilation - Production)/Production ratios). This minimizes the developmental times, and these minimized times correspond to known developmental rates at Truelove.

The R/P values computable from energy budgets, and from other sources, vary enormously. Golley (1968), speaking about the entire life cycle, concluded from early energy budget studies that about 20% of the energy assimilated by invertebrates is manifested as net production, which means $R/P = 4$. This is about triple the average total lifespan R/P values I used for Truelove invertebrates. Using these high R/P's in the model would necessitate lifespans being more than triple those presently predicted by the model. Laybourne (1976) found the opposite for the protozoan *Stentor coeruleus* Ehrenberg, with it having $R/P = 0.033$. Is it nature which has such extreme physiological variation, or is much variation due to the techniques of the observer?

The value of R/P varies with the caloric value of the animal

tissue produced. It also varies with the trophic level of the animals being evaluated. The highest value I use (for developing immatures) is 0.8 for herbivores, with lower values for carnivores and saprovores (including bacteriovores and fungivores). The R/P ratios for invertebrates, especially for microinvertebrates, which consume heterogeneous substrata containing bacteria, fungi, and soil organic matter, are virtually undetermined; and determinations of these values would be technological feats. The minimized R/P ratios are similar to those theorized by Kozlovsky (1968) in his confusing treatise on ecological efficiencies.

The death rate expression, $N = N_0 e^{-\alpha T}$, means that mortality is exponential; thus, if half of the individuals in a cohort died in a given time period, then half of the survivors will die during the next equal time period. Andrewartha and Birch (1954) used this same expression, $N = N_0 e^{r_m t}$, as the base for their popular ecological theory on the distribution and abundance of animals. The assumption is common to population growth studies (e.g. Macfadyen, 1963b; Manly, 1974; Slobodkin, 1962; Wiegert, 1974). The 8 insect life tables cited by Harcourt (1969) were highly correlated to exponential declines ($R = 0.96 - 0.99$ for all except a laboratory population at $R = 0.82$). Immatures within a taxon are normally morphologically similar, share the same resources, and experience similar environmental conditions, so are expected to have comparable mortality throughout their lives. This expression is used in lieu of having life tables for every species on the Lowland.

The growth rate expression, $W = W_0 e^{\beta T}$, is also exponential. This expression, in different notation, is identical to Brody's

(1964) $\ln W = \ln A + Kt$. It has been recently used to describe arctic insect growth (MacLean, 1973). I consider this the least justifiable of the 4 basic expressions. Growth may be sigmoid or hyperbolic, as suggested by Bottrell (1975); but even where this is the case, the straight line exponential can still approximate these growth types. Zaika (1973) stated that exponential growth is not characteristic of organisms, although it is instructive to use. I use exponential growth for growing immatures only, and express time in terms of temperature (i.e. degree days), to avoid Zaika's intended objections. Diapause or other exceptions to exponential growth can be specially considered as they become known.

These expressions apply to individuals which survive to maturity. The minimized "c" values, hence maximized growth rates, express this intent. Feeding studies give the mean responses of a population of animals, while the values actually needed are those for the fittest individuals in the population. Thus, the "c" values I use are somewhat lower than those calculated from Waldbauer (1968), and equal to or lower than others. In nature, individuals which deviate from the optima are likely to be diseased or parasitized, or to be developing under less than favorable conditions. They have a greater exposure to predation and other hazards. These are individuals which fall into the category of dying immatures. The value of "c" should increase as dying individuals expend energy reserves. Until this behavior is better defined, death is treated as occurring instantly for animals which, until death, developed optimally. These formulae may, therefore, overestimate production and underestimate respiration by slight factors.

4.5 Model Operation, and Effects of Input Variations

The model is divided functionally into 2 portions. The first is computerized, and requires 8 defined data units. It yields information about the immatures of a cohort. The effects of variations of these 8 data inputs are considered here, by comparison. The second portion is solved by use of a calculator. The information input varies for each group. I calculated energy flow through one entire cohort, then converted this to energy flow $m^{-2} yr^{-1}$ in a series of steps.

4.5.1 Model Program

The computerized portion of the model uses the same format for all invertebrates. I have listed this model program in Appendix 4. The input parameters for each cohort are: initial and final weight in μg , and initial and final surviving number, of growing immatures; "a" ($a = R/W^b$) in $nl \cdot 0_2 \cdot \mu g^{-1} \cdot hr^{-1}$; "b"; "c" ($= R/P$); and cal mg^{-1} . The output is production in cal and μg , developmental time in hours and degree days, respiration in cal and μl , and the average weight of individuals in the cohort (assuming an infinite and uniformly distributed population, continuous sampling, and 100% recovery of all stages). The calculator portion of the model uses information which must be discussed by taxon.

4.5.2 Tests of Input Parameters

Each input parameter is an approximation of a real value, which existed in the field. Cohort weight and number approximations

are crudest for lower invertebrates, and can be disputed. Other inputs will be queried, especially where they encompass dissimilar species. The purpose of these queries must be to ask "how does a change in this parameter affect final energy flow values?"

To demonstrate the effect of variations in computer inputs, I ran a series of tests using arbitrary values. A selection of these results is shown in Table 7. The examples are numbered to facilitate comparisons.

Example 1 is approximately realistic for an animal. The number range, 100 to 10, is narrow, and the respiration rate (at 12 C) is low. The R/P ratio listed can be converted to "c" by

$$(R/P) (\text{cal/g}) (4.7 \text{ cal/ml } O_2 \text{ consumed}).$$

Production in example 1 is 1.80 mg. However, the last 10 of these cohort animals, weighing 100 μg , are still alive. Therefore, the production of dead immatures in the cohort is

$$1,800 \mu\text{g} - (10)(100 \mu\text{g}) = 800 \mu\text{g}.$$

These surviving 10 individuals represent potential production, and become real production when they die. Respiration energy is lost from the system by the time the cohort number reduces to 10. The average weight, 10 μg , is that which would be found from an infinite number of samples of the developing cohort, or infinitely overlapping cohorts.

Weight variations, with the same weight range of 10-fold (examples 2-6), alter production, respiration, and average weight proportionally. A 10-fold weight range increase causes a 10-fold production, respiration, and average weight increase. Developmental time varies with the weight range. The smallest individuals, 0.001

Table 7. Effects of input variations on cohort energy flow: computer portion of the model with artificial animals

Example No.	μg/individual: Initial	Inputs							Results			
		Final	Number: Initial	Final	Respiration: a b	Tissue cal/mg	R/P*		Production mg	Respiration ml	Development Time: °C days	Average μg/Animal
1	1	100	100	10	2 0.9	6	0.587		1.80	1.35	1171	10
2	10	1000	100	10	2 0.9	6	0.587		18.0	13.5	1474	100
3	100	10000	100	10	2 0.9	6	0.587		180.	135.	1856	1000
4	0.001	0.1	100	10	2 0.9	6	0.587		0.0018	0.00135	587	0.01
5	0.01	1.0	100	10	2 0.9	6	0.587		0.018	0.0135	739	0.1
6	0.1	10	100	10	2 0.9	6	0.587		0.18	0.135	930	1
7	0.1	100	100	10	2 0.9	6	0.587		1.485	1.11	1763	5.5
8	1	100	1000	10	2 0.9	6	0.587		4.75	3.56	1111	0**
9	1	100	10000	10	2 0.9	6	0.587		18	13.5	995	2.70
10	1	100	100	1	2 0.9	6	0.587		0.475	0.356	1111	0**
11	1	100	100	2	2 0.9	6	0.587		0.664	0.498	1106	5.76
12	1	100	10	2	2 0.9	6	0.587		0.292	0.219	1195	12.8
13	1	100	2	1	2 0.9	6	0.587		0.115	0.0865	1222	17.4
14	1	100	20	10	2 0.9	6	0.587		1.15	0.865	1222	17.4
15	1	100	100	10	1 0.9	6	0.587		1.8	1.35	2342	10
16	1	100	100	10	3 0.9	6	0.587		1.8	1.35	781	10
17	1	100	100	10	2 0.5	6	0.587		1.8	1.35	20400	10
18	1	100	100	10	2 0.75	6	0.587		1.8	1.35	1797	10
19	1	100	100	10	2 1.0	6	0.587		1.8	1.35	863	10
20	1	100	100	10	2 0.9	5	0.597		1.8	1.15	995	10
21	1	100	100	10	2 0.9	6	1.174		1.8	2.70	2340	10
22	1	100	100	10	2 0.9	6	1.761		1.8	4.05	3510	10

*"c" is $(R/P)(\text{cal/g})/(4.7 \text{ cal/ml } O_2)$

**Special case: when a/B (=intermediate calculation) = 0, $\bar{W}$ computes to 0

to 0.1 μg , develop in 587 degree days, versus 1856 degree days for the largest individuals, 100 to 10000 μg . This is caused by "b". If "b" were equal to 1, then each cohort would have had the same developmental time. The effect of altering "b" can be seen in example 1, 17-19. Low "b" values make cohort development time extraordinarily long. In nature, low "b" values probably indicate inactivity.

Numerical variations (number of hatchlings versus number matured), in example 1, 8-14, have a complex, but proportional, effect on production and respiration. Developmental time increases slightly as the numerical range decreases. In examples 8 and 10, the average cohort individual was computed to have no weight. This occurs when $\alpha/\beta = 1$, a ratio computed by the model. In the special case when $\alpha/\beta = 1$, the average weight must be calculated by a second formula:

$$\bar{W} = \frac{2 N_o W_o \ln(2N_o)}{2N_o - 1}$$

Variations of "a", examples 1, 15, 16, affect only the developmental time. As "a" increases, developmental time decreases. Decreased developmental time means higher turnover rates, and, therefore, greater energy flow for the same population biomass. The value of "a" must be calculated in $\text{nl O}_2 \mu\text{g}^{-1} \text{hr}^{-1}$ for this model. If example 3 weights are converted from 100-10000 μg to 0.1-10 mg, and O_2 consumption from nl to μl , the value of "a" might be expected to be the same. It is not. In this example it changes from 2 to 1. This type of problem is inherent in using the model with values from the literature. For example, I could not duplicate the

calculations of MacLean (1973) for *Pedicia hanna* until I converted his "a" units. The model then generated his conclusions. Decreases in caloric value, examples 1, 20, decreased developmental time, and respiration loss, by a small factor. This would mean greater tissue production, but otherwise would approximately equal total energy flow, in the field.

The greatest fluctuation in energy flow occurs when the R/P ratio is increased, as in examples 1, 21, 22. Production remains constant, but respiration and developmental times double when the R/P doubles. High R/P ratios cause long lifespans, and decrease yearly production, in the field. I used minimum R/P values for Truelove invertebrates (4.4).

Taxonomic, and nutritional differences, and imprecise measurements, make the cohort weight ranges of Truelove invertebrates impossible to specify without being arbitrary. The effect of overlapping choices of weight ranges can be considered through examples 1, 6, 7. Here, 2 possible population states, with the same weight ranges, can exist: 7) one species with a weight range of 0.1 - 100, and 1, 6) equal total numbers of 2 species, one with a weight range of 0.1 - 10, and the other 1 - 100. The field population numbers, and biomass, are identical for these populations, as are all input parameters for the species. The mean weight of example 7 individuals is 5.5 μ g. The mean weight of 1 and 6 individuals is the same, $\frac{1}{2} (10 + 1) = 5.5$ μ g. The cohort production of example 7 is 1.485 mg. The developmental time of example 7 is 1763 C degree days, distinctly longer than example 1 and 6. The 1763 degree days, example 1 produces $(1763/1171)(1.8) = 2.71$ mg, and example 6 produces $(1763/930)(0.18) =$

0.34 mg. Half their combined production of 3.05 mg is 1.53 mg. The production by an example 7 population is 3% less than an ostensibly identical population with examples 1 and 6 parameters. Respiration is also 3% less. Therefore, the effect of arbitrary weight ranges will be minor, as long as these ranges are similar to the actual ranges of real invertebrates.

The above example shows little energetic differences, but may show significant strategic differences between the 2 populations. Take the simplest reproductive case as an example (a case most easily discussed, but the conclusions are similar for all cases). The 10 mature individuals in each cohort do not feed, and their bodies contain the eggs for the next generation. For example 7, this means there is $100(0.1) = 10 \text{ } \mu\text{g}$ of reproductive tissue, from $10(100) = 100 \text{ } \mu\text{g}$ of adults, leaving $990 \text{ } \mu\text{g}$ of adult tissue for mating dispersing, and ovipositing. In example 1, $100 \text{ } \mu\text{g}$ of reproductive tissue from $1000 \text{ } \mu\text{g}$ of adults leaves $900 \text{ } \mu\text{g}$ for activities. Example 7 individuals expend 1% of their stored adult energy on egg production, while 1 and 6 expend 10%. Therefore, example 7 adults have a proportionally greater amount of energy to expend on placing the next generation in an optimal environment. These apportionments of energy for reproduction are alternate strategies for exploiting similar resources, by ostensibly similar animals.

4.6 Limitations

The model results are not actual measurements. They are predictions based on a combination of measurements and assumptions about the behavior of invertebrate populations. I call these model

predictions "hypotheses." The model, and especially the model parameters, may be reinterpreted in light of additional evidence. Since energy flow is presently not a measureable phenomenon, the model predictions cannot be compared to actual energy flow values. These "hypotheses" are my best estimates of energy flow.

These equations are used to calculate production and respiration of Truelove Lowland invertebrates developing under Truelove conditions. Temperatures there are low, and do not fluctuate widely during the growing season. Most of the invertebrates of Truelove develop under aquatic or semiaquatic conditions. I have not examined the use of these equations in southern environments.

Chapter 5

INVERTEBRATE POPULATIONS

Energy flow data in this thesis are separable into objectively measured quantities, and into quantities which are actually hypothetical. Hypothetical data are discussed in Chapter 6. Objective energy flow data includes the results of standing crop measurements, respiration measurements, dietary studies, etc. This chapter treats invertebrate standing crops at Truelove, and measured features of invertebrate populations related to energy flow.

For this analysis, I separated invertebrates into 3 categories, based on how their populations were sampled. The largest category is soil dwelling invertebrates. These are animals active at or below the soil surface throughout their lives. The other 2 categories are pterygote insects, and field-layer inhabitants. There is overlap in these divisions: but they are made to organize data presentation, not to be exclusive.

5.1 Soil Invertebrates

All Truelove invertebrates, except spiders and some herbivores, inhabit soil for part, or most, of their lives. Aquatic invertebrates are considered to be soil inhabitants, although they may live in water above the soil surface. In Chapter 2.3., I outlined the major problems of sampling soil dwelling invertebrates. They must be extracted from soil by methods of uncertain efficiency. The

significance of the extracted populations is not immediately evident. A cryptobiotic population can numerically equal one with a rapid turnover, but energy relations of the 2 differ greatly. These problems are examined here.

5.1.1 Standing Crops

The standing crop is the quantity of living invertebrates inhabiting an area. It is expressed m^{-2} , and in the tundra biome is usually given as a seasonal or yearly figure. In warmer climates, where population levels fluctuate more widely, monthly fluctuations are commonly reported (e.g. Willard 1973 a-d, and Riegert and Varley, 1973).

Standing crops have been reported by invertebrate investigators at all IBP tundra sites (Behan(1973 unpubl.), Bowen (1972), Bunnell et al (1975), Chernov (pers. comm.), Flower-Ellis (1973), Holding, Heal, MacLean, and Flanagan (1974, and unpublished reports at this same IBP invertebrate working group meeting, Fairbanks, Alaska, 1973), Kauri et al (1969), Rosswall and Heal (1975, and unpublished reports at this same V IBP international meeting on biological productivity of tundra, Abisko, Sweden, 1974), Solhøy (1972), Whittaker (1973 unpubl.), and Wielgolaski and Rosswall (1972)). The Truelove site researchers were expected to make a similar contribution.

5.1.1.1 Extraction Efficiencies of Funnels

The efficiency of any extraction is less than 100%. Comparative efficiencies of different arthropod extraction techniques vary widely, and vary from taxon to taxon (Edwards and Fletcher, 1971).

Absolute extraction efficiency, determined by adding animals to sterile soil cores, also varies. O'Connor (1967) reported 95% recovery of enchytraeids with his funnels, but Willard (1972) recovered only 48% with these funnels. Willard found that Salt-Hollick flotation recovered 20% of the Collembola and Acarina added to defaunated soil cores. Losses must occur during collection of soil cores, through injuring or trapping of soil animals.

In this study, soil cores were taken to a depth of 5 cm. The population existing below this level must also be determined. Thus, the extraction figures given by my techniques (5.1.1.2) underestimate actual standing crops. These numbers must be increased if estimates of the actual numbers, and biomass, of the soil invertebrate standing crops are to be reasonable.

5.1.1.1.1 Materials and Methods

In 1971, I extracted 15 soil cores, to depths of 15 cm at 5 cm intervals, from 3 locations, with my Tullgren funnels. Simultaneously, I extracted 48 similar soil samples, from these same sites, using the simple Baermann system.

In 1972, I compared extractions by my Tullgren, Baermann, and O'Connor funnels, to those of a Macfadyen high gradient extractor (operated by Jan Addison, at Truelove), a nematode extractor (operated by Dennis Procter, at Truelove), and Salt-Hollick flotation, and nematode flotation (supervised by Dr. John Willard, at the University of Saskatchewan). For this, I randomly collected 8 sextets of soil cores each, at the raised beach and meadow sites. Soil cores in a sextet appeared similar, and were taken adjacent to one another. I immediately extracted 3 sets of cores in my extractors, gave 2 sets

to Addison and Procter, and sent 2 sets to Saskatoon. Dr. John Willard's technicians extracted 9/10 of each core by Salt-Hollick flotation, and 1/10 by centrifugal flotation (for nematodes). Paraffin oil, used in the flotation process, was washed off with xylene before individuals were dried and weighed.

I attempted several absolute extraction efficiency experiments, similar to those done by Willard. For these I extracted Collembola, enchytraeid worms, and nematoceros Diptera larvae, with Tullgren and O'Connor funnels. I added these animals to defaunated soil cores, then re-extracted them several hours later. For nematoceros Diptera I added 23 larvae to 6 soil cores, allowed 2 hr. for equilibration, and then re-extracted.

5.1:1.1.2 Results, and Interpretations

The extraction results for cores taken to depths of 5, 10, and 15 cm are shown in Table 8. In this table, Acarina and Collembola results were extracted by use of Tullgren funnels, while those for other taxa are from Baermann funnels. Virtually the entire population of organisms extractable by dry funnels were from the top 5 cm. With the Baermann funnels, there was a similar, but less pronounced, dominance of the top 5 cm. In the meadow extractions, water inflow, which occurred while the cores were being taken, probably washed surface inhabitants into the lower depth cores. In a similar experiment, with cores taken to 7.5 cm at 2.5 cm intervals, using a Macfadyen high gradient extractor, Addison (1975) found approximately 80% of all Truelove Collembola to be in the top 2.5 cm, and approximately 95% in the top 5 cm.

Table 8. Comparative depth extractions, 1971. Numbers of invertebrates at depths of 5, 10, and 15 cm

sample Date	Core Depth	Substrate, and location	Nematoda	Enchytraeidae	Crustacea	Acarina	Collembola	larval Diptera
VIII-20	0-5 cm	Raised beach,	126	1	1	35	271	0
	5-10 cm	Beschel Hill	114	3	0	1	71	0
	10-15 cm		157	7	0	2	3	0
VIII-23	0-5 cm	Intensive	449	16	143	29	22	51
	5-10 cm	Study	8	0	6	0	0	4
	10-15 cm	Meadow	4	0	0	1	0	1
VIII-25	0-5 cm	hydric	407	12	314	7	15	46
	5-10 cm	Meadow	70	2	37	3	1	5
	10-15 cm		32	2	8	0	0	1

Appendix 5.A.B shows the results of the comparative soil core extractions, 5.A giving numbers m^{-2} , and 5.B giving mean biomass m^{-2} . Procter's extractions were not completed, while Addison's and Willard's samples were extracted after delays. The variation within-sample sextets was as great as between-sample variation. This obscured extraction differences. The Baermann funnels gave the lowest population values, and so were the least efficient extraction technique. Willard's (1972) value of 20% absolute recovery of Collembola by flotation cannot be used to estimate Truelove populations, because Truelove soils are different from prairie soils, and hence extraction efficiencies may differ. It does suggest that Collembola populations can be greater than any of these extraction procedures indicate.

A further comparison, of Acarina and Collembola recovered from Tullgren, Macfadyen, and Salt-Hollick processes, is shown in Table 9. This table shows test populations m^{-2} , and the seasonal populations m^{-2} as measured by Tullgren and Macfadyen extractions. The mass/individual extracted is also given here. At the raised beach, large numbers of younger (smaller weight) Collembola were extracted by both the Macfadyen and Salt-Hollick methods. At the meadow, these 2 methods yielded similar numbers of individuals but of smaller weight, than the Collembola extracted by Tullgrens. With both the Macfadyen and Salt-Hollick samples, the soil cores were stored for approximately one month prior to extraction. Probably, the Collembola population structure changed, and a "baby boom" occurred during storage (cf. Edwards and Fletcher, 1971). The seasonal mean populations of Collembola collected by the Macfadyen apparatus were greater than those collected by the Tullgren funnels.

Table 9. Acarina and Collembola populations m^{-2} : 1972 season means, and comparative soil core extractions

	Tullgren Funnels		Macfadyen Hi-Gradient		Salt-Hollick	
	Acarina	Collembola	Acarina	Collembola	Acarina	Collembola
No. $\mu g/ind.*$	No.	$\mu g/ind.$	No.	$\mu g/ind.$	No.	$\mu g/ind.$
<u>Raised beach</u>						
season mean: 4899	5.8	16578	3.3	6912	18221	5.3
test mean: 3737	4.6	4191	7.5	6185	7.7	35654
					3.1	4231
					18.9	28049
						1.7
<u>Meadow</u>						
season mean: 3231	4.3	2070	10.8	13039	8737	4.9
test mean: 3685	6.4	1969	7.6	1414	12.0	1591
					3.3	1726
					23.6	1471
						2.0

*No. = number of animals m^{-2} ; $\mu g/ind.$ = μg oven dry wt. of average individual collected

Variations exist in the Acarina data. The heavy individual weights from the Salt-Hollick flotation may be due to paraffin remaining within the body of a mite despite the xylene wash. The Macfadyen extractor yielded higher seasonal population estimates than the Tullgren funnels; but Addison did not weigh these Acarina, so their biomass could not be estimated from her samples.

The absolute extraction efficiency experiments gave unsatisfactory results, except for nematoceros Diptera larvae. Twelve larvae were recovered, of 23 added, giving 52% recovery. Collembola collected on water, as I did for the first extractions, will bloat; they should have been collected on moist plaster (Healey, 1971). Ruptured enchytraeid worms were found on the metal screens below the soil cores after the second extraction, but these were rarely found here following normal extraction. Thus, Collembola and Enchytraeidae were water-logged by the time of the first extractions. Consequently, I have reported only the Diptera extraction results.

5.1.1.1.3 Conclusions

Results of the depth extractions showed that most Truelove invertebrates inhabited the top 5 cm of the soil. Free-swimming Crustacea, recovered below this depth, were flushed there when the samples were collected. The extraction comparisons showed that Baermann funnels were less efficient than O'Connor funnels; and that Tullgren funnels were less efficient than the Macfadyen High Gradient apparatus. Comparison of these results with those obtained by Salt-Hollick flotation, and the known low absolute efficiency of this method, suggested that actual populations were higher than those

recovered by any techniques used. The recovery rate of introduced Diptera larvae, 52%, again indicated that absolute recovery efficiencies were low.

Use of some correction factors is required if actual populations are to be estimated. I assumed a correction factor of 1.5-fold for Enchytraeidae, and Diptera larvae, which is $2/3$ that used by Willard (1972), and $2/3$ my own Diptera recovery rate. For Rotifera and Tardigrada, the correction factor used was 2-fold the counted population. This allowed for counting errors, and for less efficient extraction, of these minute animals. Rotifera counts at the meadow site were increased 20-fold, because results obtained during the Protozoa standing crop counting procedure (Chapter 6.1) indicated that they had a much higher standing crop than O'Connor funnels revealed. Crustacea were increased by 1.2-fold, largely to compensate for their being leached out of soil samples when the cores were collected. For Collembola I used Addison's (1975) Macfadyen extraction results, without modification. Acarina population numbers, obtained from Tullgren extractions, were increased 2-fold at the raised beach and 3-fold at the meadow, to equal the numbers collected with the Macfadyen extractor. Their Tullgren-collected biomass was increased by the same factors.

All correction factors, and corrected population figures, are shown in Table 10. These correction factors were used to convert populations in the top 5 cm to actual populations m^{-2} . Data presented here, and from literature sources, would justify the use of higher values. However, the smallest individuals of a species are most likely not to be collected - the smaller the body, the greater

the relative distance required to escape a soil core. Thus, estimation of population numbers should require the use of larger correction factors than those needed to estimate population biomass. I am not aware of any published literature which justifies making differential corrections. To avoid overestimating population biomass, I use these minimal correction factors. Their use gives conservative estimates of actual invertebrate population numbers.

5.1.1.2 Materials and Methods

Standing crop data, for 1972 (Table 10), were collected from single 5 x 5 m plots at each of the 2 main study sites. Data for 1970-71 were collected from similar plots at these same sites, from 8 other lowland sites, and from the plateau. These sample sites, sample sites discussed later in this chapter, and the Truelove Lowland itself, are shown in Figure 5.A.B.

Standing crops were determined from O'Connor, and modified Tullgren, funnel extractions. O'Connor funnels (O'Connor, 1962, 1971) were used to extract 5 cm deep x 6.1 cm diameter soil cores, halved in to 2.5 cm sections. Sixty-eight full-size cores from the raised beach, and 64 from the meadow, were extracted by this method in 1972. In 1971, simpler Baermann funnels were used to extract 264 soil cores, 24 at a time. Tullgren funnels were used to extract 42 unsplit cores from each site, 7 cores at a time, in 1972. In 1971, 194 cores were extracted, of which 28 samples were spilled or lost. Preliminary sampling in 1970 was done with Tullgren funnels having vented tops. Subsequently, Tullgrens were covered with unvented, 31 cm diameter barn lamp shields, and heated by 25 watt light bulbs for

Fig. 5. Maps of Truelove Lowland

A. Place names and general topography of the Lowland.

Emergence trap locations are referred to in code (Chapter 5.2.1).

These are: ISSM and ISSRB, Intensive Study Site Meadow, and Raised Beach; MesM, Mesic Meadow 1 km from southeast corner of Water Lake; MesM-2, Mesic Meadow 1 km east Water Lake; NCampM, xeric meadow 200 m north of base camp; BesH, Beschel Hill; E.W.L., meadow 100 m east of Water Lake; S.W.L. and N.W.L., 3 traps at south end, and 2 traps northeast, of Water Lake, about 100 m from shoreline; HydM, Hydric Meadow (permanent standing water) 2 km west of base camp.

B. Sample sites referred to in Chapter 5

△ 1971 emergence trap sites
(4 traps/site)

□ 1971 pitfall trap sites

▲ 1972 emergence trap sites
(5 traps/site)

■ 1972 pitfall trap sites
(bar indicates series
of 4-5 traps)

○ 1971 soil sample sites
(11)

□ 1970-73 sweep net sites

● 1972 soil sample sites
(2)

C. Collection sites of 290 *Gynaephora* larvae and pupae

Unit	% Area	No. Captured
Salt water lagoons	0.6	-
Raised beaches	3.3	165
Limestone pavement	5.0	71
Rock outcrops	14.0	-
Water bodies	21.7	-
flat		18
Meadows:	55.4	
drained		36
		290

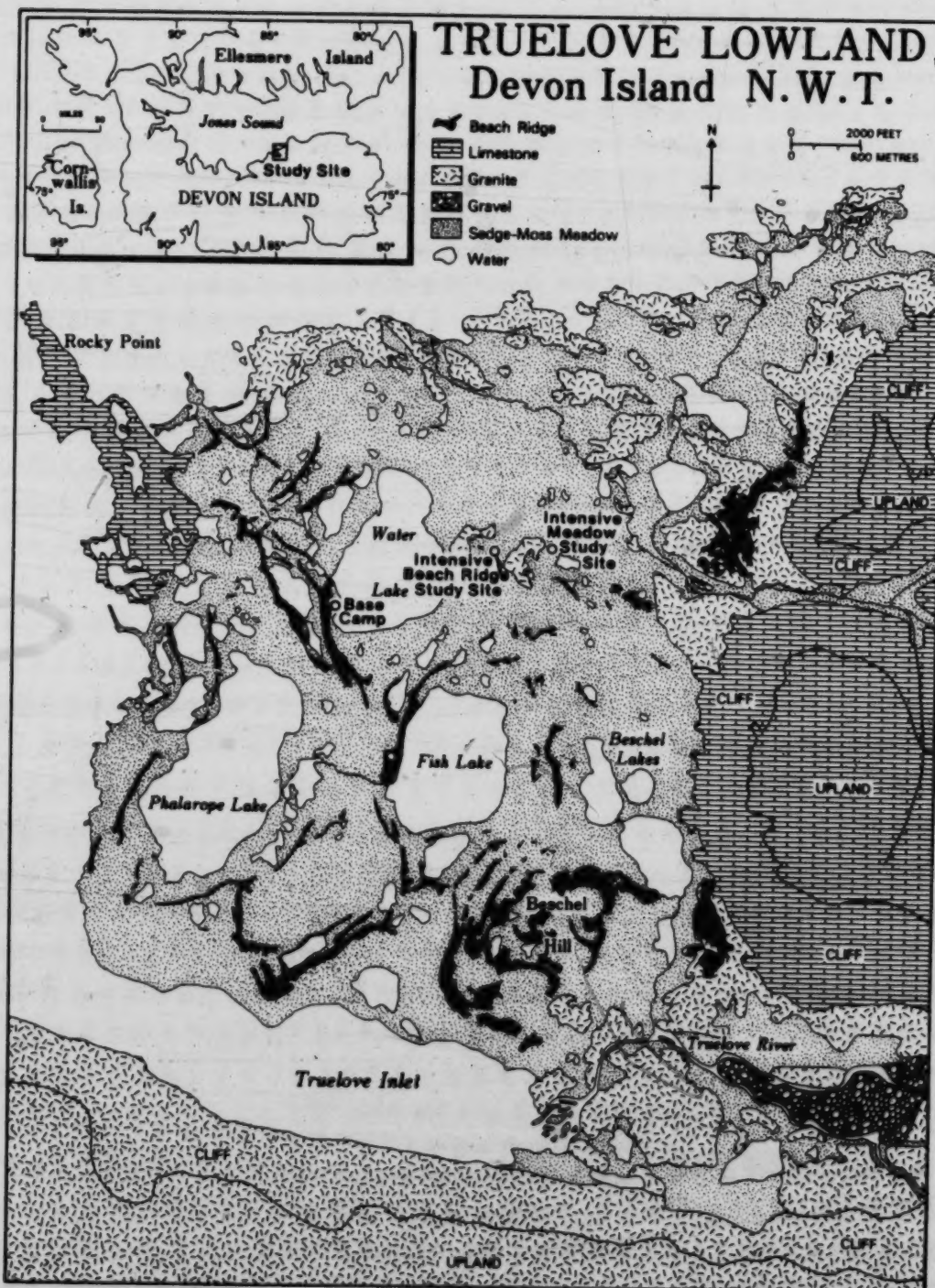
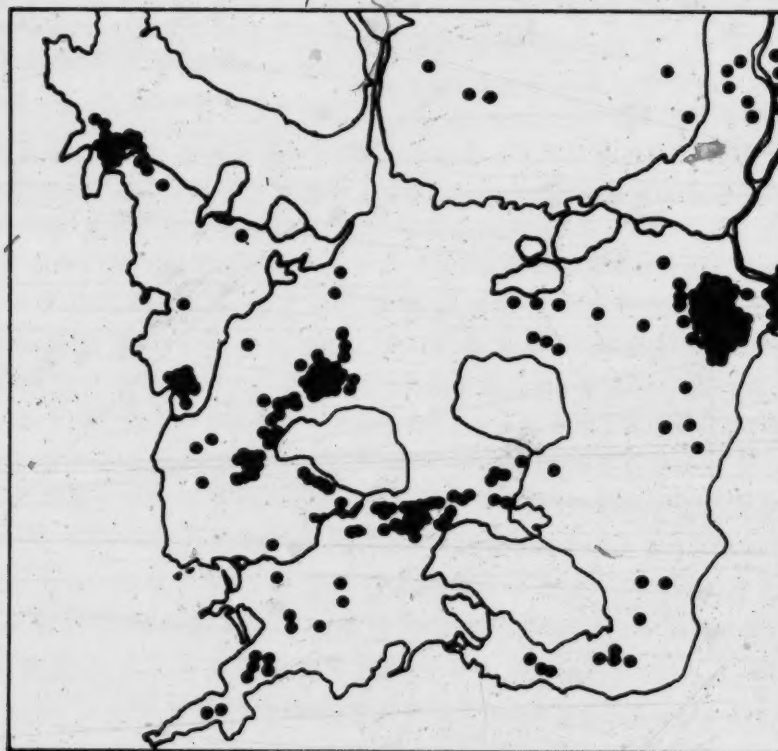
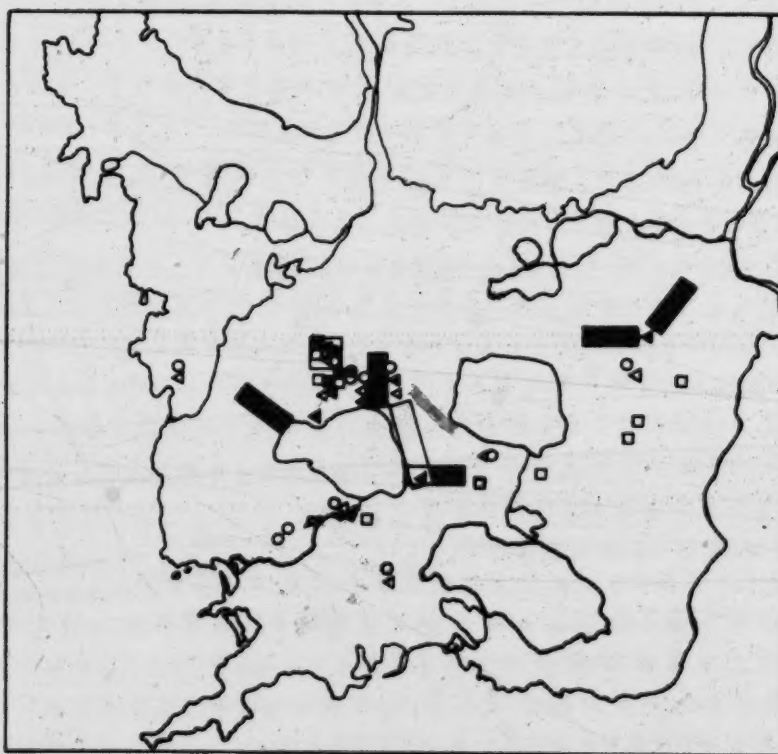


Fig. 5.A. Place names and general topography of the Truelove Lowland.



C. *Gynaephora* collection sites



B. Sample sites

36-48 hr. until the soil core was completely dry. After the soil thawed to 5 cm, 1972, soil cores were randomly collected, on each plot, at 5 day intervals throughout the summer. In 1971, cores were collected from July 15 (thaw) to August 25, at approximately 3 day intervals. All cores were cut with a tapered gladiolus planter, placed individually in plastic bags, carried to the laboratory via backpack, and were usually in the extractors within 8 hrs. Extractions were preserved in ethyl alcohol. Animals collected in 1972 were counted, oven-dried, and weighed on a taxon per sampling date basis. Subsequently, these were lumped to give mean numbers (arithmetic and geometric), and confidence limits, and mean biomass, m^{-2} for the entire season. In 1971, extractions were counted but not weighed.

5.1.1.3 Results

The 1972 seasonal average standing crops, for all invertebrates (except Protozoa and Nematoda), are given in Table 10. These results are given as the arithmetic mean $\pm$ S.E., and geometric mean ($\log n + 1$ transformation) with 95% confidence limits. Collembola results are from use of a Macfadyen extractor; Acarina data from use of Tullgren funnels; and Enchytraeidae through to Cladocera, and Diptera from O'Connor funnels. Araneida, Lepidoptera and Hymenoptera determinations are explained in Sections 5.2 and 5.3. Correction factors, discussed in the preceding section, are also included, along with the corrected arithmetic mean population numbers, and biomass. I use these corrected mean populations for the model.

The 1971 extraction results have been published (Ryan, 1972). These samples were collected from 11 places on the lowland, and so

Table 10. Invertebrate standing crops m⁻² at the study sites, 1972

Component	Enchytraeidae	Rotifera*	Tardigrada	Copepoda	Ostracoda	Cladocera	Acarina	Araneida	Collembola	Insect larvae:	Lepidoptera	Colleoptera	Diptera:	Tipulidae	other Nematocera	Cyclorhapha	Hymenoptera
Raised beach																	
Numbers collected,	5791	110	2836	0	0	0	4899	0.3	18221	0.2	0	0	0	0	263	8	8
mean ± S.E.	±471		±469				±863								±97		
Numbers collected,	4537	75	1620				2315		11700						193	7	7
geometric mean	(4019	(15	(1147				(1302		(8400						(132	(0	(0
(fiducial limits)	5856)	132)	2244)				3958)		16500)						260)	17)	17)
Dry weight collected, mg	119.8	0.006	2.92				28.4	3.87	96.8	0.774					8.25	7.53	0.51
Correction factor	1.5	2	2				2		-						1.5	1.5	
Estimated actual population	8690	220	5670				9800		18220						395	12	8
Estimated actual biomass, mg	180	0.01	5.8				57		96.8						12.4	11	0.5
Meadow																	
Numbers collected,	18632	321	1158	19264	496	5	3231	1.8	8737	0	0	4.9	7076	35	7076	35	1.8
mean ± S.E.	±1455	±57	±154	±3904	±226		±526						±919	±12	±919	±12	
Numbers collected,	14640	201	754	5838	162	3	1688		4700			3	4447	25	4447	25	
geometric mean	(11901	(124	(556	(3771	(77	(0	(982		(3400			(0	(3393	(5	(3393	(5	
(fiducial limits)	18070)	289)	995)	9010)	263)	10)	2776)		6500)			10)	5800)	43)	5800)	43)	
Dry weight collected, mg	395	0.01	1.19	24.6	0.48	0.04	13.2	1.18	42.6			30.7	64.5	2.6	64.5	2.6	1.33
Correction factor	1.5	20	2	3.2	1.2	1.2	3		-			1.5	1.5	1.5	1.5	1.5	
Estimated actual population	27500	6400	2300	23100	595	6	9690		8740			7	10600	52	10600	52	2
Estimated actual biomass, mg	590	0.2	2.4	29.5	0.58	0.05	40		42.6			46	96.8	3.9	96.8	3.9	

*Rotifer mass is estimated

indicate diversity in the standing crops on the lowland. These extractions were made using simple Baermann funnels (which were later found to be inefficient) and Tullgren funnels, whose efficiency varied with meadow and raised beach soils. Because of these factors, 1971 results were not used for the energy flow model.

5.1.2 Turnover Rates

Growth rates determine rates of change of the standing crop, i.e. turnover rates, and hence energy flow rates. To determine turnover rates, I set up a series of experiments, similar in principle to putting *Gynaephora* larvae in emergence traps for a season to determine their growth. I autoclaved muskox dung, and also collected winter dung before any invertebrates were active. About 125 g of dung was added to each of 10 16 oz. jars, and 30 fine mesh silk or polyester bags. These were inoculated with mycelia of 5 species of fungi isolated from muskox dung: *Cylindrocarpon didymum*, *Humicola* sp., *Penicillium* sp., *Phoma* sp., and an undetermined species tentatively called hyaline dark. Inoculated dung was incubated until fungal growth was visible and extensive. I extracted Collembola and Acarina by use of Tullgren funnels, nematoceros Diptera larvae with simple Baermann funnels, and enchytraeids and nematodes with O'Connor funnels. These animals were separated into size categories, and I added 10-20 individuals of one size category to each jar or bag, while preserving an equal number of the same size individuals in alcohol. Enchytraeid worms and nematodes went into jars, while the others went into 23 bags, leaving 7 empty control bags. The jars were left on a raised beach, and the bags buried flush to the surface

in meadow soil. They remained undisturbed for $1\frac{1}{2}$ - $1\frac{1}{2}$ seasons, then were re-extracted.

Results were unsatisfactory. Animals were recovered from the control bags (which should have been empty), and taxa other than those introduced were found in the test bags. Evidently, the mesh of the bags was not fine enough to keep out invaders. No enchytraeids were recovered from the jars - I presume that the initial extraction and handling weakened them, and that they died before becoming established. In one jar there was an equivocal success: a jar into which 10 mature nematodes had been introduced, and held for 1 season, had 3 middle size nematodes and 1 adult. They were too small to weigh (cf. Procter, thesis in prep.). The results suggest that individuals of this species of nematode can undergo one life cycle in $1\frac{1}{2}$ - 2 field seasons. Thirty-six Collembola were recovered from a jar into which 10 individuals had been introduced. The size range of individuals recovered was too great for constructive comment on their growth rates.

These experiments, repeated with modified jars placed in the soil, would have yielded the information sought. The present results do not answer many questions about turnover rates.

5.2 Pterygote Insects

The airborne bodies of winged insects command visual attention, usually to the neglect of their earth-bound counterparts. The winged adult is a specialized, comparatively ephemeral stage, of an otherwise terrestrial insect. Its mobility makes it a prey object for other ecosystem components, and allows the transfer of its body nutrients

from the larval habitat, to other habitats. Since this study was part of an integrated ecosystem project, my responsibilities included examining certain relationships of invertebrates to other ecosystem components. The winged insects were prime foci for information requests. In this section I examine some of these ecosystem related problems, as well as the subject of insect energetics.

Pterygote insects have been collected with a vacuum apparatus at several IBP sites (Kauri, Moldung, Solhøy, 1969; Odum, 1971, p. 18; Riegert and Varley, 1973; Carpelan (pers. comm., IBP desert biome)). This collecting technique is generally unsatisfactory, due largely to the difficulty of relating the catch at any one time to a specific measure of production m^{-2} . Sweep net sampling of insects has been used in energy budget studies (e.g. Smalley, 1960), but this procedure might better be used to indicate relative abundance (Southwood, 1966). Winged adult insects, emerging from soil and vegetation, are the clearest indicator of production m^{-2} . Winged insect emergence is a type of potential production, which can be used as a measure of adult production, and by extrapolation, of all life stages (cf. 2,3.2). Adults can be collected in emergence traps, but these are not commonly used because tall, dense or rapidly growing vegetation interferes with their efficiency, preventing their use in most areas.

5.2.1 Emergence Traps

Insect emergence traps have been used at an IBP meadow site (Olechowicz, 1971), and at the Pt. Barrow tundra site to collect adult *Pedicia hanna* (Diptera, Tipulidae) (MacLean, 1973). Aquatic insect adults are collectable in emergence traps (Mundie, 1956), and have

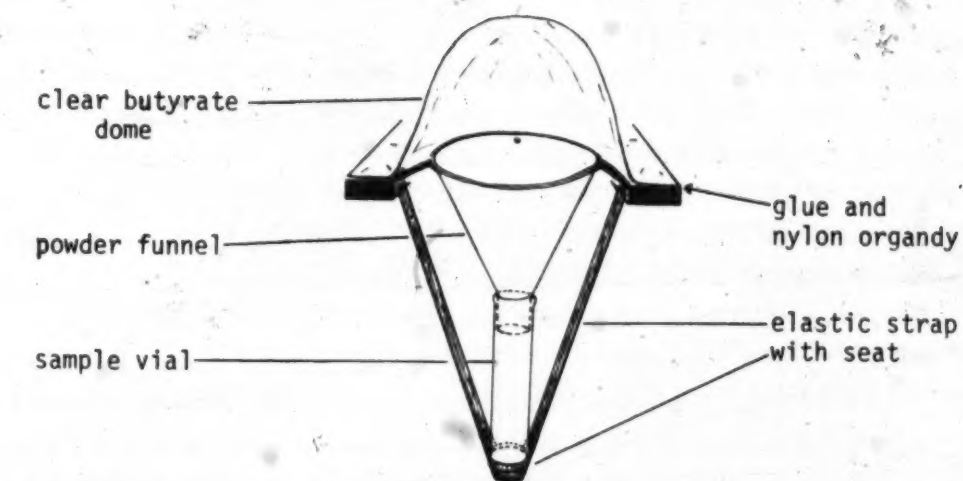
been collected as measures of production (McCauley, 1975; Mundie, 1973; Welch, 1973). Emergence traps were used to sample aquatic insect production at the Truelove Lowland (Minns, 1977).

I used emergence traps to measure the production of winged insects at Truelove in 1971-72. Tundra vegetation is ideal for emergence trapping as it is low, thin, and grows slowly.

5.2.1.1 Materials and Methods

My emergence traps were 1 m² wood frame pyramids (Figure 6.B) similar to those described by Beirne (1955). The sides were nylon screen (12.3 mesh cm⁻¹), with one side zippered for access. Internal seams and joints were sealed with nylon organdy strips (36 mesh cm⁻¹) and glue to prevent insect escape. Flaps of muslin sheeting, held down by rocks and dirt bags in 1971, and buried in place in 1972, kept insects from escaping from beneath the traps. Traps were guyed with nylon ropes to resist foehn winds. Each trap had a clear, butyrate plastic dome top 16.5 cm in diameter (Figure 6.A). A 100 ml powder funnel centered below the dome funneled falling insects into a vial containing 95% ethyl alcohol. This vial was held in place by an elastic strap.

In 1971, 4 traps were placed in each of 5 meadow and 4 raised beach sites (see Figure 5.B). In 1972, 5 traps were placed in each of 6 meadow and one raised beach site. Traps were maintained at both intensive study sites both years, and at 4 subsidiary study sites in 1971, and 2 in 1972. The collecting vials were changed every 4-7 days, depending on the intensity of emergence. At the end of each season, all traps were examined for spiders and dead flies, which were



A



Fig. 6. Emergence trap for winged insects. A. Detail of trap top. Funnel bolted to 4 tin strips allowed catch vial to be held tightly by elastic strap. B. Trap on raised beach slope, 1971; 1972 trap bottom flaps were buried in place. Note torn screen, and cut anchor rope, by arctic fox.

collected whenever found. The 1971 collections were sorted and counted. In 1972, the collected insects were sorted, counted, oven-dried at 80 C for 48 hr. (to a constant weight), and weighed.

5.2.1.2 Results

In 1971, emergence traps were set out after insects had started to emerge. Twenty-one trap bottles (of 36) spilled during the first trapping period. Arctic foxes chewed and cut all but 2 of the nylon guy lines which anchored the traps against wind, and destroyed 2 traps (Figure 6.B shows a fox chewed trap). Subsequently, on August 5 a foehn wind (c.a. 90 km hr^{-1}) destroyed 3 raised beach traps, and shifted others. Insects collected in several traps could not have emerged inside the trap, e.g. specimens of the lake caddisfly *Apatania zonella* Zett. and the blowfly *Protophormia terraenovae* (R.D.). Thus, part of the 1971 data was spoiled, or suspected of being contaminated.

Traps at the intensive study sites, and at 3 meadow sites, functioned properly. Graphs of the numbers of insects collected per trap period (Ryan, 1972) show that the intensive study site traps were functional before the season peak catch, while those of other sites were functional at, and after, the peak. Thus, the 1971 intensive study site results may be compared to 1972 results. Table 11 gives seasonal emergence m^{-2} for the operational 1971 traps, and, for comparison, 1972 results from the intensive study sites, and from a mesic meadow site - this last site being compared with reservations.

In 1972, emergence trapping was completed without problems. Results are given in Table 12.A.B as seasonal total per trap, of

Table 11. Emergence traps. Mean numbers of insects and spiders collected $m^{-2} yr^{-1}$ in 1971, and comparative 1972 values*

comparative 1972 values*

Trap location and year	Total winged insects	Lepidoptera Geometridae	Chironomidae	Sclariidae	Diptera					Hymenoptera			Araneida
					Tipulidae	Mycetophilidae	Empididae	Dolichopodidae	Muscoidea	Tenthredinidae	Ichneumonidae		
ISSM													
1971	373.5		350.25	7					8.5		5.5	1.25	
1972	908.4		887.4	5.2	0.8			0.4	12.8	0.8	1	1.8	+ 0.2 egg cases
ISSRB													
1971	91.75		82.5	1.75			0.25		5.25	0.5	1.5	0.5	
1972	82.4	0.2	72.8	3.4	0.6		1.8		2.8	0.2	0.6	0.2	
MesM													
1971	180.25		144.5	5.5	0.25	1		0.75	23.25		5	2	+ 0.75 egg cases
1972	181.6		79.8	96.6	0.2	0.4	0.4		4.2			0.6	+ 0.2 egg cases
MesM-2													
1971	173.5		139.75	11.5	0.25	0.5		0.5	9.5		8.75	0.25	
NCampM													
1971	352.25		328.25	9					9.75		5	0.25	+ 0.5 egg cases

*1971 means of 4 traps, 1972 means of 5 traps

Table 12. Emergence traps, 1972. A. Biomass of winged insects and spiders collected $m^{-2} yr^{-1}$

Trap location and number	Total winged insects	Diptera							Hymenoptera			Araneida	
		Lepidoptera Geometridae	Chironomidae & Sclariidae	Tipulidae	Trichoceridae	Mycetophilidae	Empididae	Dolichopodidae	Syrphidae	Muscoidea	Tenthredinidae	Ichneumonidae	Lycosidae
ISSM-1	61.48	43.26							18.22				3.05
-2	40.94	38.57			0.33				1.53	0.84			0.43
-3 Vac*	67.93	28.76			0.33				36.38	0.84	1.62		0.61
-4 Vac	63.32	34.34					2.83		22.88	2.04	1.32		0.61
-5 Vac	36.97	22.59			0.66				14.05				1.22
ISSRB-1	6.86	4.72							2.14				
-2	9.14	3.11	3.87			0.53			1.23		0.40		
-3 Vac	4.85	2.14		0.34					2.37				
-4 Vac	13.12	4.18		0.34	1.05				3.06	3.06	1.43		
-5 Vac	12.85	2.16	8.32		0.53				1.84				0.61
DesH-1	3.10	1.63							1.47				
-2	3.18	1.34		0.34					1.50				
-3 Vac	15.79	2.91	8.66	3.04					1.18				
-4 Vac	26.66	19.06			3.60		1.92	1.88					
-5 Vac	21.09	8.60					7.71	4.78			27.95	1.65	
MesM-1	37.12	36.57		0.22	0.33								
-2	22.17	20.84						1.33					
-3 Vac	40.29	17.60				3.61		19.08					
-4 Vac	20.35	12.68						7.67					
-5 Vac	13.73	8.00						5.73					
E.W.L.-1	33.65	16.96						16.25		0.44			0.61
-2	27.23	19.48		0.23		3.35		3.57		0.60			
-3 Vac	6.86	5.26		0.23	0.33			0.64		0.40			
-4 Vac	10.71	8.86		0.23				1.62					
-5 Vac	23.73	8.67		0.23				4.35	10.48				3.66
S.W.L.-1	23.06	12.41			0.33			10.02		0.30			1.83
-2	15.94	8.62						7.32					2.44
N.W.L.-1	12.21	11.82						0.39					1.22
-2	33.53	22.70			0.33			10.03		0.47			3.66
-3	21.90	8.34						13.09		0.47			1.22
HydM-1	39.36	34.44						4.92					
-2	39.36	34.44						4.92					1.65
-3	17.05	13.33			0.33			2.94		0.47			1.22
-4	57.46	41.88						15.58					2.44
-5	99.31	41.70			0.33			54.24		4.04			1.65

#Values are mg oven dry weight

*Vacuumed when trap bottles were changed

Table 12 (con't) Emergence traps, 1972. B. Numbers of winged insects and spiders collected $m^{-2} yr^{-1}$

Insects and spiders collected in yr		Diptera										Hymenoptera		Araneida		
Trap location and number	Total winged insects	Lepidoptera Geometridae	Chironomidae	Sciaridae	Tipulidae	Trichoceridae	Mycetophilidae	Cecidomyiidae	Empididae	Dolichopodidae	Syrphidae	Muscoidea	Tenthredinidae	Ichneumonoidea	Lycosidae	Linyphiidae
ISSM-1	1132		1120									12				5
-2	917		904	9		1						2	1		1	egg case
-3 Vac*	872		836	10		1						22	1	2	1	
-4 Vac	1040		1015	3					2			15	2	2	1	
-5 Vac	582		562	4		2						13		1		2
ISSRB-1	118		110	5								3				
-2	70	1	58	6					2			2		1		
-3 Vac	59		54	3		1						1				
-4 Vac	103		89	3		1			3			5	1	2		
-5 Vac	62		53		1				4			3				1
BesH-1	32		29									3				
-2	34		24	5		1						4				
-3 Vac	81		59	10	1	9						2				
-4 Vac	181		170	4					2		2	3				
-5 Vac	170		149	10							7	4			1	2 + egg case
MesM-1	287		101	184		1	1									
-2	183		59	123								1				
-3 Vac	169		102	54					2			11				
-4 Vac	166		85	76		1						5				
-5 Vac	102		52	46								4				1
E.W.L.-1	369		353	4								11		1		1
-2	328		255	64		1			2			5		1		
-3 Vac	109		99	5		1	1					1		2		
-4 Vac	160		150	6		1						3				
-5 Vac	294		275	13		1						4	1			6
S.W.L.-1	328		310	11								7				3
-2	178		141	28			1					7		1		4
N.W.L.-1	341		337	2								2				2
-2	601		551	37			1					11		1		6
-3	342		320	7								14		1		2
HydM-1	1105		1097						1			7				
-2	301		300				1									2 + egg case
-3	350		344				1					4		1		2
-4	1027		1012						4			11				4
-5	834		802				1					25		6		2 + egg case

*Vacuumed when trap bottles were changed

numbers (12.A) and biomass (12.B) collected. These results are summarized as biomass m^{-2} mean, standard deviation, and Standard Error in Appendix 6. Chironomidae and Sciaridae, and Muscoidea (= Anthomyiidae and Muscidae), are combined in the dry weight data. Truelove sciarids are slightly larger than the average chironomid; their relative abundance, usually low, can be determined at each site from Table 12.A. When few individuals of a taxon were collected, they were weighed together for several sample periods. Their values are given as (mean weight/individual)x(no. individuals) for each trap.

In both seasons, most chironomids emerged in the first weeks following thaw, sciarids over a longer period, and muscoids throughout the season.

Araneida are listed in Table 12.A.B. These are standing crop values, not emergence production. They are presented here because they were collected from emergence traps. These data are discussed in Section 5.3.

The data in Tables 11 and 12 can be compared to emergence data elsewhere, e.g. for the 2 meadows in Poland (Olechowicz, 1971). There 1473 winged insects, weighing 1857.3 mg (dry weight), emerged m^{-2} from the uncultivated meadow during the 6 summer months. Diptera accounted for 48% of the number, and 19.5% of the biomass, while Hymenoptera were, respectively, 10.2% and 1.6%. The Truelove meadows averaged 449 insects, weighing 33.2 mg, $m^{-2} yr^{-1}$. Thus, Truelove meadows produced 1.8% the insect mass of this Polish meadow in one season. Truelove Diptera comprised almost 100% of the numbers, and 95% of the biomass, while Hymenoptera were, respectively, 0.2% and 4%.

Comparisons may be made with comparative terrestrial data, which should become available through the IBP.

5.2.1.3 Trap Collection Efficiency, and Thermal Characteristics

Many queries can be made about these emergence traps and their operational efficiencies, particularly since the trap top is an original feature, and because this type of trap is infrequently used. My emergence traps operated on the principle that insects emerging within a trap flew to the dome, fell into the funnel, and were preserved. Insects were captured shortly after emergence; otherwise, adult metabolism would cause weight loss. Temperature and growth conditions within a trap were approximately the same as those outside. Each of the above statements was tested, and the results are given in this section.

5.2.1.3.1 Taxa Collected

By observing the taxa collected, I found insects which could not have emerged from within several 1971 traps. This led me to squelch the results of 10 1971 traps: 2 with known entries, and 8 suspected "unsealed" traps. Additionally, I squelched the results from 6 moved or damaged traps.

Insects obviously were caught in the traps, but did a significant number avoid being trapped? My first tests consisted of putting sweep-netted flies into spare 1971 traps, then determining the traps' capture efficiency. These flies were of uncertain age, and were probably injured by the sweep-netting, so the approximately 50% recapture rate was inconclusive. At the conclusion of the 1971

season, I cleaned the sides, corners, and ground within each of the 32 standing traps, using a 12 volt, battery-powered automobile vacuum cleaner. Eight flies and 8 spiders (Linyphiidae) were collected. The 8 spiders presumably killed flies, thus reducing trap collections, but this test indicated no other inefficiencies.

In 1972, I vacuum cleaned 3 traps, in each of 5 locations, every time I changed the trap vials. These results (designated 3-5 Vac) are included in Table 12.A.B. I analysed this data as insect biomass collected per trap, and as number of insects at each vial change, per trap. The data were not normally distributed, so I transformed them by $\log(n + 1)$. This gave a normal distribution when plotted on probability paper, thus permitting parametric statistical analysis. A one-way analysis of variance test, used to compare the biomass in vacuumed versus non-vacuumed traps, indicated that there were no significant differences between the biomass collected on either raised beaches, or meadows. I compared the numbers of insects collected in vacuumed versus non-vacuumed traps by site, using Goulden's (1952) unequal sample size correction, and a two-way analysis of variance test. For the Beschel Hill traps, the F-ratio was significant ($p = 0.05$); otherwise there were no significant differences. All traps had been set-up while the ground was still snow-covered. At thaw, I realized that 2 Beschel Hill traps had been placed on raised beach ground, one on a transition zone, and 2 on a meadow. Comparing the last 3 vacuumed traps, to the first 2 unvacuumed, was actually comparing raised beaches to meadows. The difference found at Beschel Hill was predictable because of trap site differences.

No significant differences were detected between comparable vacuumed and non-vacuumed traps. However, spiders, and presumably insects with damaged wings, were removed by vacuuming. Insects collected by vacuuming (approximately 40% of the total) had less time to metabolize energy reserves than those which flew into the collecting bottle. Therefore, vacuumed traps were expected to yield greater numbers, and biomass, than non-vacuumed traps. These predicted differences were masked by variation between trap catches. Because no significant differences were found, the hypothesis that winged insects were effectively collected by the funnel mechanism is correct.

5.2.1.3.2 Adult Weight Variation

The weights of insects collected in the emergence traps lie between their emergence, and starved to death, weights. Actual weight lost by capture time could not be determined. The maximum prepupal biomass is required for the model. Individuals of *Gynaephora*, weighed as prepupae, had metabolized 29% of this biomass by the time they became pharate adults, and lost 43.5% by the time they emerged as adults (3.4.2). What weight loss occurs with flies?

I collected approximately 350 apparently young puparia of *Protophormia terraenovae* (R.D.) (Calliphoridae). From these I selected 252 healthy looking puparia, and randomly sorted them into 3 groups. Group 1 was oven-dried immediately, while groups 2 and 3 were put in sleeve cages and examined daily. Group 2 adults were killed and oven-dried at emergence; group 3 adults, starved and offered only water, were collected and oven-dried at death. Caloric

values were determined for each group, and are shown in Table 13. Caloric values were virtually the same for each group. Flies at emergence weighed 75%, and at death 36%, of their pupal biomass. This information is discussed further in Chapter 6.

5.2.1.3.3 Trap Microenvironment

I looked for possible microenvironmental changes within traps. When meadow site traps were removed, the vegetation under them appeared slightly greener than that surrounding them. This greenhouse effect was not visible at a distance, did not affect the vegetation height, and was not observed on raised beaches.

In 1973, I placed 11 copper-constantan thermocouples in, and around, an emergence trap positioned on a south-east facing raised beach. Eight of these were paired, one of each pair being placed inside, and the other outside, the trap. Pairs were glued inside *Gynaephora* cast skins, placed inside white paper towel rolls (simulated Stevenson screens), buried 1 cm below the gravel ground surface, and exposed over plants. Temperatures were monitored through a variety of weather conditions using a Leeds and Northrup millivolt potentiometer.

The temperature results appear in Appendix 2. I analysed the paired results using Wilcoxon's non-parametric signed rank test. The cast skin and exposed thermocouple pairs were not significantly different. The paper roll pairs were significantly different, showing that air temperatures within the trap were warmer ($p = 0.01$; about 1 C warmer). Soil temperatures within the trap were significantly cooler ($p = 0.02$; about 1 C cooler). These conflicting results have a simple

Table 13. Comparison of puparia, newly emerged adults, and starved-to-death adults of *Protophormia terraenovae* (Diptera, Calliphoridae)

Stage	No. Individuals	Mean Dry weight	cal g ⁻¹ (ash free)
Pupa	84	7.34 mg/pupa	6445
Adults, newly emerged	49	5.54 mg/adult	6402
Adults, starved to death	59	2.65 mg/adult	6452

explanation. The soil surface is heated directly by insolation, and the subsurface is then warmed by conduction. The trap shaded the soil within, decreasing insolation, thus decreasing the subsurface temperature. The trap itself acted as a greenhouse, retaining rising convection currents which would otherwise be dissipated by wind. This produced warmer air temperatures. Soil within the traps was not heated effectively by convection currents. Since cast skins had the highest temperatures, color and physical characteristics of an object were more important than being inside or out of the trap. Conditions within a trap differed from those external, especially when the sun was shining. These differences were slight, and should be less than those measured here, as Truelove is normally hazy or cloudy during the growing season. The hypothesis that temperatures within traps, versus those external, are great enough to alter insect emergence rates is disproven by these data.

5.2.2 Terrestrial Versus Aquatic Emergence

Terrestrial insect emergence may differ significantly from that of water bodies. Total emergence recorded at Char Lake (400 Km west of Truelove, on Cornwallis Island) was $143 \text{ mg m}^{-2} \text{ yr}^{-1}$ (Welch, 1973), which is 4-fold that of the average Truelove meadow, and 19-fold that of the average raised beach (c.f. Appendix 6). A pond at Pt. Barrow, Alaska, produced 300 mg m^{-2} of chironomid adults (Bierle, 1972).

Since lakes and ponds cover 22% of the Truelove Lowland area (Bliss, 1975), differential emergence could affect the Truelove ecosystem in several ways. Greater insect production could affect the distribution of insectivorous birds. In this regard, Pattie (1974)

studied energetics of the Lapland longspur, *Calcarius lapponicus*, at Truelove. Adults of aquatic insects could return significant amounts of mineral nutrients to land bordering lakes. Nutrient mineral additions can dramatically increase tundra plant production (Haag, 1974). Nutrient flows, especially that of nitrogen, are important components of this IBP study (Babb, 1974). Stutz (1972) reported Truelove nitrogen fixation rates of $0.42 \text{ mg N m}^{-2} \text{ yr}^{-1}$ at the main raised beach site, and $16.7 \text{ mg N m}^{-2} \text{ yr}^{-1}$ at the main meadow. As insects are 10% (dry weight) nitrogen (calculated from Spector, 1956), it became imperative to examine their possible role in nitrogen flow on the Truelove Lowland.

5.2.2.1 Sweep Net Sampling

I took sweep net samples over much of the Lowland in 1970, and in selected sites in 1971-72. Each sample was collected by making 100 - 180° sweeps close to the ground with a 30 cm diameter net having 90 cm handle, and held at arm's length. All samples reported here were taken during calm weather while insects were flying. In 1970, 65 sweep net samples from isolated land areas - not containing ponds or bordering lakes - contained a mean 68.4 (s.d. 52.5) insects, of which 83% were chironomids. Thirty-two of these samples averaged 34.0 mg dry weight. In areas immediately adjacent to the 3 largest lakes on the Lowland, 55 sweep net samples averaged 800.9 (s.d. 2603) insects, of which 98.1% were chironomids. Fifteen of these samples averaged 189.3 mg dry weight. Sweep samples near lakes contained 12-fold the numbers, and 6-fold the biomass, of samples from pondless land areas.

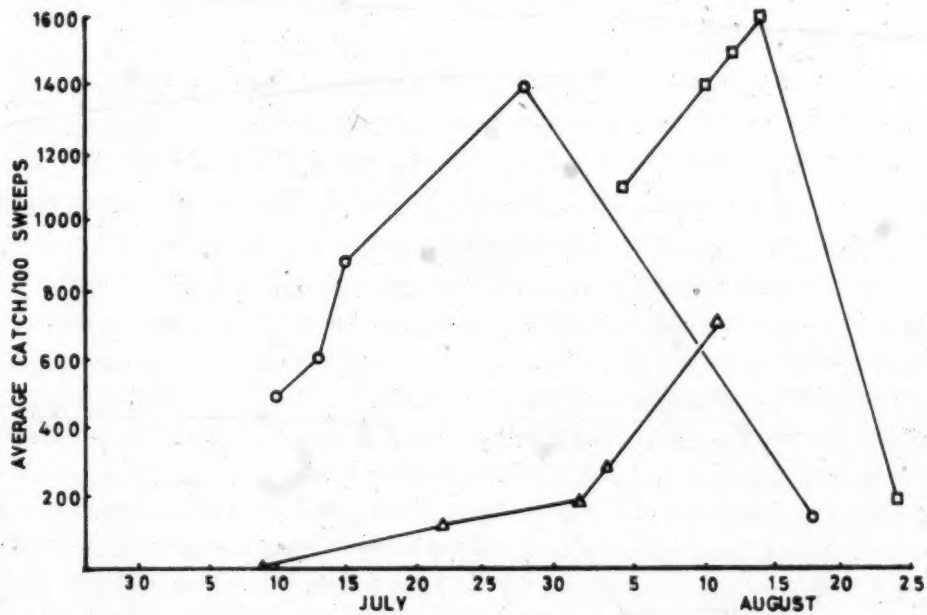
To determine if these differences occurred yearly, I took

sets of 5 samples at the south end of Water Lake, and sets of 3 samples at the land-locked Intensive Study Site Meadow, each year from 1970-72. The results, in Figure 7, showed that this was an annual phenomenon. The last 1972 sweep samples taken at Water Lake, on August 11, showed this sample date to be the yearly peak catch. This day was followed by cold weather, which precluded further sampling. Because water bodies do not cool as rapidly as land, aquatic chironomids continued to emerge. The day I left Truelove, August 20, was clear and calm, and it probably would have been the peak catch date had I been able to sample.

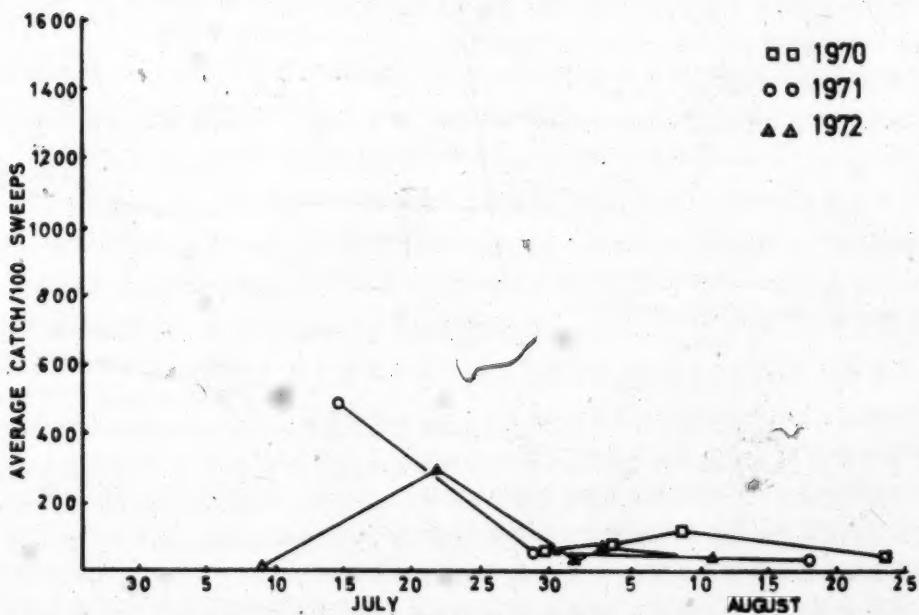
The peak 1970-72 sweep net catches were taken between July 30 and August 11. Emergence trap data showed that peak terrestrial insect emergence occurred earlier, shortly after thaw. From this data I conclude that the aquatic insect emergence peak was later, as well as larger, than that of terrestrial emergence.

5.2.2.2 Floating Lake Traps

From July 27 to August 1, 1971, I placed 8 1 m^2 floating screen traps 6, and 12, m from shore of Water Lake. Two each were put at the north, east, south and west ends. I meant to compare the numbers of insects caught by these to numbers caught in pitfall traps placed at 50 m intervals from these points (except west), to determine where the lake chironomids were dying. The floating traps were destroyed by wind and ice, but during their short period of operation the catch 6 m from shore was about 50% greater than that at 12 m. The north and west traps contained numerous (average 850) chironomids of terrestrial origin, while those of the south and east contained



A. SOUTH OF WATER LAKE



B. INTENSIVE STUDY SITE MEADOW

Fig. 7. Insects caught by sweep net sampling. A. Meadow near water body (each point is 5 sets of 100 sweeps). B. Land-locked meadow (each point is 3 sets of 100 sweeps).

larger aquatic chironomids (average 250, with 200 pupal skins).

Terrestrial insects were blown into the north and west sides of the lake, and aquatic insects off the south end onto the land.

5.2.2.3 Pitfall Traps

If lake insects fell onto the surrounding land, this fall should be collectable; furthermore, it should be accompanied by greater spider populations in the fall zone. To investigate this hypothesis, in 1972 I buried cake pan pitfall traps, 22 x 22 x 5 cm, at 50 m intervals on transects extending north, east, and south of Water Lake, and west and south of pondless Beschel Hill.

Results of this trapping are shown in Appendix 7. The lake transect pitfall traps accumulated an average 1.0 g of insects/trap, while Beschel Hill traps collected 0.8 g/trap. The difference is too small to analyse further. Spiders appeared to have a greater biomass at Beschel Hill, contrary to the predicted distribution. But, these were mostly individuals of *Tarentula exasperans*, a large, wandering spider not common in meadows. The meadow linyphiids were sedentary web spinners. Thus, for spiders the traps provided an activity - not an abundance - index.

Each spring, spiders were a major dietary component of several Truelove bird species (Pattie, 1972). These birds selectively feed in areas of high prey density, thus reducing prey abundance. The spider abundance question becomes tautological. It does not resolve the problem of insect transfer to land. The same tautology exists when considering insect deadfall, that concentrated bird feeding around lakes may depress the collectable insect population. Pattie (pers.

comm.) and Taylor (1974) reported concentrated insectivorous bird feeding activity around arctic lakes.

5.2.2.4 Aquatic Emergence Traps

Water Lake insect emergence was monitored in 1973 by Minns (1976). The total emergence he recorded was 374 cal m^{-2} (at 5.6 cal mg^{-1}), which is $66.5 \text{ mg dry weight}$. The last sample date was August 9, when the lake reached its maximum temperature. This date was earlier than the date of the seasonal peak sweep net catch around Water Lake for 2 of 3 years. Minns stated that the total Water Lake insect emergence could equal that of Char Lake (400 km west of Truelove), which was $143 \text{ mg m}^{-2} \text{ yr}^{-1}$ (Welch, 1973). The winged insect production measured in 10 traps placed in adjacent north, east, and south Water Lake meadows was $20.9 \text{ mg m}^{-2} \text{ yr}^{-1}$. Average meadow emergence was $33.2 \text{ mg m}^{-2} \text{ yr}^{-1}$, while raised beaches produced 7.6 mg m^{-2} . Water Lake production was 3 to 6-fold greater than that of its bordering land. It is at least 2-fold the average meadow, and up to 19-fold the average raised beach, winged insect production.

5.2.2.5 Conclusions

Since winged insect populations were higher around lakes than in land-locked meadows, and because lake production rates were higher, an insect transfer from lakes to land does occur. The floating trap catches indicated that this is influenced by prevailing winds, which blow terrestrial insects onto, as well as off, Water Lake. The deadfall of insects around Water Lake was not notably greater than at the land-locked control site, nor were spider populations. Insectivorous birds reduced deadfall insect and spider populations; and insect

dispersal further reduced the pitfall trap catch.

Where these insects die, and decompose to mineral nutrients, is uncertain. If lake emergence were 5-fold greater (measured: 2 - 17-fold) than land emergence, and if these insects were blown over, and died on, an area of land equal to that of their home lake, their bodies would add 10 mg of nitrogen $m^{-2} yr^{-1}$. In meadow soils, a mean (1971-72) 250 mg of nitrogen are fixed $m^{-2} yr^{-1}$ (Stutz, 1974). Therefore, the nitrogen added to land from lakes is 4% of the yearly land nitrogen fixation. Initial nitrogen fixation rates reported by Stutz (1972) were considerably lower, and approximately equalled this insect nitrogen inflow. I undertook this investigation partly to substantiate insect importance in nitrogen flow, given Stutz's earlier figures. The significance of this exercise pales considerably in the light of his initial error. Lakeside chironomid densities apparently affected bird feeding patterns, but these flies did not add sufficient nutrients to the soil for them to be considered important factors in nitrogen cycling.

5.3 Field-layer Arthropods

The term field-layer applies where foliage immediately above ground surface, as in grassland or herbage, creates a distinct habitat. The field-layer is a reduced habitat in the Arctic, particularly at Truelove where foliage seldom exceeds 5 cm in height. Here it is occupied only by larval sawflies and Lepidoptera, and by spiders. Populations of these groups were sampled by soil extraction, and with emergence traps, so they were treated in preceding sections. Both require further consideration.

In 1970, I sampled these arthropods by randomly dropping a $1/2 \text{ m}^2$ rectangular frame 10 times on raised beaches, meadows, and other communities. Altogether, I sampled 870 m^2 , collecting representatives of 7 spider species. The standing crop of *Tarentula exasperans*, which averaged 58 mg live, was $0.033 \text{ individuals m}^{-2}$ in meadows, and 0.22 on raised beaches. Linyphiid spiders, averaging 2 mg live, had $0.1 \text{ individuals m}^{-2}$ in meadows, and 0.025 m^{-2} on raised beaches; however, I found only 19 of these spiders, and 45 webs. The approximate dry weight for *T. exasperans* was 17 mg, and was 0.6 mg for linyphiids. One *Gynaephora* larva, 4 larvae without secondary setae, and one lepidoptera pupa were found on drier sites, particularly on raised beaches. These results were used in the *Gynaephora* standing crop determination (3.8). I did not determine whether the "naked" larvae were Lepidoptera, or Hymenoptera Symphyta, which limits the value of these results. Therefore, I used adult Tenthredinidae, and the single *Psychophora sabini* (Lepidoptera) adult, collected in emergence traps as the base for my energy flow calculations in Chapter 6. The standing crop predicted by use of emergence trap data was approximately 40-fold greater than the total standing crop determined by use of drop frames.

Tullgren extraction funnels did not recover spiders. They either escaped, or the 0.26 m^2 total surface sampled with Tullgrens was too small to pick any up. The average individual of *T. exasperans* collected in the 34 1972 pitfall traps weighed 16.2 mg dry (831 specimens); the average linyphiid weighed 129 μg dry (5726 specimens). In 1972 emergence traps, the $1.8 \text{ linyphiids m}^{-2}$ of meadow, and 0.2 m^{-2} of raised beach, weighed 658 μg each; no individuals of *T. exasperans*

were collected in traps at eight location, except in 1971, when a cast skin of this animal was found at the raised beach.

Individuals of *T. exasperans* averaged 17.5 mg dry weight in the drop frame samples, and a comparable 16.2 mg in pitfall trap samples. A large proportion (70% in 1970-71) of pitfall collected spiders were adult, mostly males, seeking mates as well as prey (Leech and Ryan, 1974). Hence, pitfall trap results did not represent a random cross-section of the population structure; apparently, the drop frame procedure gave an even more biased sample. Both sampling methods under-represented the immature population. The standing crop of *T. exasperans* shown in Table 10 is that found by use of drop frames, 0.22 individuals, = 3.87 mg, m^{-2} of raised beach.

Linyphiid webs outnumbered spiders 2.4-fold in the drop frame sample. These spiders were virtually invisible when not in their webs. Thus, their standing crop was probably underestimated by the drop frame procedure. The meadow emergence trap linyphiid population was $1.8 m^{-2}$, considerably greater than the drop frame value of $0.1 m^{-2}$. The average linyphiid in the drop frame sample weighed 600 μg , and 658 μg in emergence traps. The pitfall average weight was 129 μg . Dispersing immatures, and wandering adults, were collected in pitfall traps, while most spiders remained in their webs. So, again, the pitfall traps did not provide useful information about the average individual mass in the population. I used the emergence trap results, the largest of the 2 population samples, for the meadow standing crop results given in Table 10.

Chapter 6

ENERGY FLOW AT TRUELOVE

Energy flow defies precise measurement. I estimated it at Truelove using a mathematical model, described in Chapter 4, and standing crops of each group of Truelove invertebrates, given in Chapter 5. This chapter contains the energy flow calculations. I explain model parameters by taxon, and discuss the calculations. Since this information cannot be explicitly proven, I call it a hypothesis. I also include other hypothetical information, on the elementary structure of this ecosystem, in this chapter.

6.1 Protozoa, a Special Case

Since Protozoa would have otherwise been ignored in the overall IBP study, I included them in my own research project. In this section I explain how I treated them, and why.

Quantitative studies of Protozoa have not yielded meaningful population energy flow measurements (Heal, 1971). Their results do suggest that annual protozoan production is greater than that of larger invertebrates (Macfadyen, 1963a). Comparatively small changes in their population numbers, or biomass, may be associated with greatly accelerated metabolic turnover, where micropredation takes place (Stout, 1973). Aquatic soil environments are transitory in most habitats. Consequently Protozoa, capable of rapid growth, have a distinct advantage in filling flooded niches (Stout and Heal, 1967). Otherwise, Protozoa normally constitute a relatively

insignificant part of the total terrestrial microbial, and animal, biomasses. In an arctic tundra pond at Pt. Barrow, Alaska, Protozoa were found to be important bacteria grazers, and among the most important components of the microfauna (burrowing micrometazoa were comparably important) (Fenchel, 1974). Data from this study, and others at the same site (Barsdate *et al* 1974, Hobbie, 1972), show that the microfauna are significant energy flow factors. An energy budget for a ciliate protozoan (Laybourn, 1976) represented an important step in the calculation of protozoan energy flow.

On August 5, 1972, Dr. O.W. Heal, with my assistance, made a brief examination of Protozoa in the Intensive Study Site meadow soil. We counted the numbers of Protozoa from 4 cm^3 blocks of meadow "hollows" soil by rinsing several drops of distilled water through each block, then examining this flush water in a haemocytometer (volume 400 μl). The numbers found were increased by a factor of 5.10^4 , to give an estimate of the standing crop m^{-2} to a depth of 5 cm. These counts were rounded off to the nearest 0.5. Standing crop biomass was estimated from adult dry weights of related Protozoa from other areas (Heal, 1971). Then Heal estimated the probable number of generations yr^{-1} of each protozoan group. Yearly tissue production was computed from these estimates. Then, it was assumed that for each calorie of tissue produced, 2 calories were respired. These standing crops, number of generations, and energy flow values are shown in Table 14.

The Protozoa energy flow estimates are quite tentative. Tissue production is estimated to be $1.5 \text{ g m}^{-2} \text{ yr}^{-1}$, and the total energy flow was $105 \text{ kJ m}^{-2} \text{ yr}^{-1}$. When these values were calculated,

Table 14. Protozoa standing crop and energy flow estimate, meadow site

Taxon	Est. adults m^{-2}	Adults/mg dry weight	Est. gen. yr^{-1}	Est. tissue produced	Est. Joule flow m^{-2}
Flagellates - naked amoebae	1.5×10^8	10^6	6	900 mg	65000
Ciliates	1.0×10^6	10^5	6	60 mg	4000
Testates	5.0×10^7	2×10^5	2	500 mg	36000
				1500 mg	105000

Heal felt that they should be given as $\pm 10X$ of the value determined. This, however, is an arbitrary error range; the true answer could lie outside of the range. We disagreed on one assumption. Heal felt that for every calorie of tissue produced, about 4 calories should be respired. I chose a more conservative value of 2 cal respired, which is closer to the R/P ratios used for other groups of animals.

There is evidence to support my Protozoa energy flow proposal. On June 21, I clipped several hand fulls of frozen *Carex* sp. tops, and put these in a quart jar with boiled water, and left the jar outside on the snow. On July 12, 1972 I set up a 2 part experiment to determine increase and starvation times of Protozoa under Truelove conditions. The purpose of the increase experiment was to find the increase rate of Protozoa under conditions of abundant food and minimal predator impact. Three vials containing 135 mg of air-dry chopped *Carex*, *Salix*, and *Dryas* leaves, and 25 mg of dry muskox dung, were mixed with 10 ml boiled water. Eight hours later, the numbers, and types, of Protozoa in 10 drops of this infusion were counted under a 25X dissecting microscope. Counts were repeated every 12 hours for 3 days. For the second part, starvation rates were determined by adding 5 drops of *Carex* infusion broth, visibly teeming with Protozoa, to 3 vials each containing 10 ml of boiled water. Ten drops of each vial were examined simultaneously with those from the increase experiment vials. Between counts, all vials were capped, and stored outside for exposure to normal Truelove weather. Water levels were maintained by adding boiled water to replace drops removed for counting.

The increase and decrease rates are shown in Figure 8.A.B. There were 5-9 population doublings in 72 hours, so the doubling time ranged from 14-8 hours. These were mostly minute flagellates. Specimens of a large *Euglena*-like species underwent 3 doublings. In the starvation experiment, most individuals were *Euglena*-like. Most disappeared by the end of day 2; however, at the end of the experiment I still found individuals on the bottoms of the vials. The population half-life was initially 16 hr., decreasing abruptly with time.

Results of this experiment prove that protozoan populations can increase, and die off, quite rapidly, under normal Devon Island conditions. There were more doublings in 3 days than in the protozoan energy flow proposal for all summer. Their rapid disappearance, when starved, shows how quickly the produced Protozoa biomass can disappear. Meadows are completely innundated for several weeks following spring thaw, providing field conditions comparable to those of this experiment.

My predictions of Protozoa energy flow can be tested by use of the computer model. Assuming a respiration rate of $3.5 \cdot 10^4 \mu\text{l hr}^{-1} \mu\text{g}^{-1}$ (pooled data from Heal, 1971, extrapolated to 12 C by $Q_{10} = 2.5$), a growth increase of 2.5-fold, and other inputs as used above, one population doubling requires 31 degree days. This approximation would permit 10 generations yr^{-1} in the meadow. At the least, it suggests that the number of Protozoa doublings yr^{-1} can be more than the proposed 6, 6, and 2. The Protozoa calculation is the only instance where I use less than the model predicted number of generations yr^{-1} .

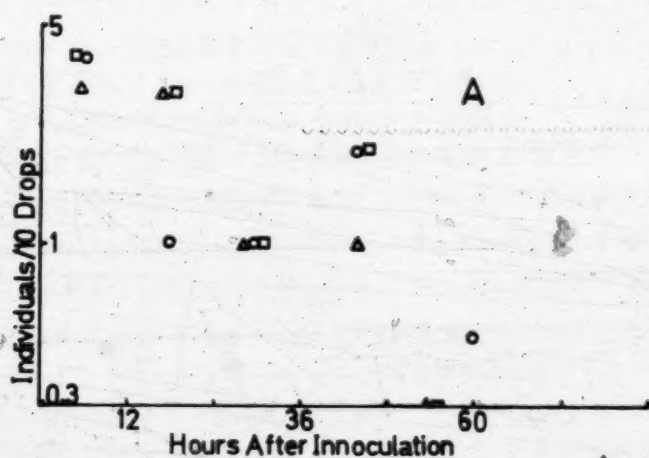


Fig. 8. Maximized
Protozoa increase and
decrease rates at the
Truelove Lowland.

A. Protozoa decrease in
clean water, i.e. with-
out food. The population
half-life is initially
16 hr, decreasing with
time.

B. Protozoa increase in
Carex infusion, i.e. with
excess food.

a. Number of generations
= $A (2^x)$:

○ $1 (2^x) = 27 \quad x = 5$

□ $3 (2^x) = 750 \quad x = 8$

△ $3 (2^x) = 2000 \quad x = 9$

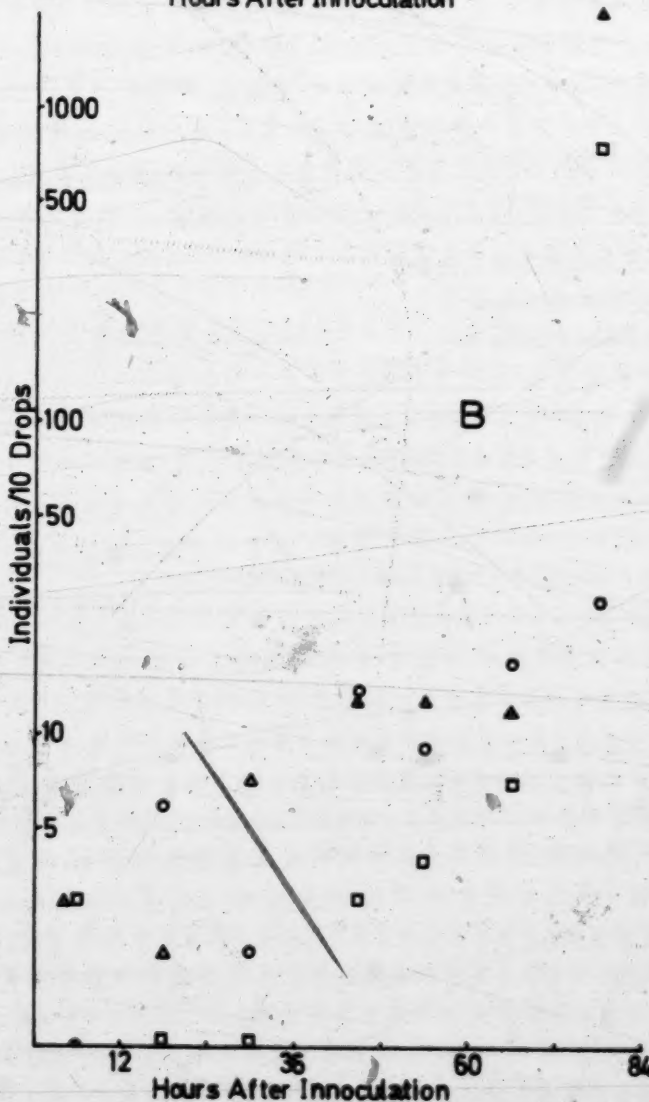
b. Generation time:

○ $72 \text{ hr}/5 = 14 \text{ hr}$

□ $72 \text{ hr}/8 = 9 \text{ hr}$

△ $72 \text{ hr}/9 = 8 \text{ hr}$

c. Log phase generation
time = 4.5 hr



The biomass of soil Protozoa at Pt. Barrow attained levels of $0.005-0.15 \text{ g m}^{-2}$ in the upper 1 cm of soil (Bunnell *et al* 1975). The Truelove meadow standing crop in the upper 1 cm was a comparable 0.082 g m^{-2} . Therefore, the single Truelove sample probably does not grossly misrepresent the actual populations. Fenchel (1974) found that about 80% of the pond Protozoa at Pt. Barrow occupied the top 2 cm of pond bottoms. If a similar distribution existed in Truelove meadows, then the Protozoa standing crop and energy flow values will be half the values given in Table 14. Protozoa population sampling techniques currently used are crude, with unknown efficiency of recovery. Both Alaska investigators reported the actual populations recovered. However, sampling inefficiency could be greater than the correction factor I used to estimate the population to 5 cm.

The yearly production of fungi and bacteria is a bit less than half the yearly net primary production (Whitfield, 1977). Both of these groups of organisms are potential food for Protozoa. The Protozoa energy flow total is approximately 3% of the meadow net primary production. Thus, the known ecosystem parameters do not contradict the proposed Protozoa values, and would permit these values to be larger, without conflict.

The raised beach site is exposed and well drained. Conditions at this site do not favor protozoan development. No Protozoa counts were made here. The nematode population of the raised beach site was 3-fold that of the meadow (Procter, 1977b). Bacteria-feeding nematodes and Protozoa compete, and the Protozoa are important regulators of nematode populations, especially where soil water contents are high (Sohlenius, 1968). I presume that the nematodes have a competitive

advantage over the Protozoa at the raised beach site, and that here the Protozoa energy flow is much less than at the meadow.

This Protozoa energy-flow estimate is crude. The single sample date, the few samples taken, and the large number of assumptions demand a wide error range for the Protozoa energy flow values. Had I directed my entire research effort at this group, my conclusions about them would still require the use of more assumptions than were used with higher invertebrate taxa, and would still be tentative. The obstacles to estimating Protozoa energy flow are so complex under simplified Truelove conditions, that I feel an accurate estimate in a temperate climate may be technically impossible to make.

6.2 Model Results, by Taxa

The computer and calculator inputs for each Truelove invertebrate taxon, and the calculated outputs, are shown in Appendix 8.A-C. The value of "b" is universally taken to be 0.87 (see Section 4.4). The "c" values listed incorporate the conversions from tissue calories to respired calories, as well as the R/P ratios. The model inputs for each group, including the structure of cohorts, are independently considered here. Most values discussed in this section appear in, or are derived from, this appendix.

Appendix 8.A-C also shows intermediate steps in the computations. Some of these are model-generated predictions about the analysed populations. Many of the predictions are testable through comparison with data obtained in the field, which I do in this section. Energy flows, which were determined through the calculations here, are discussed separately in 6.3 - 6.4.

Appendix 8.D.II contains cumulative seasonal temperatures recorded from the meadow and raised beach sites. It shows the mean yearly temperatures at - 1 cm, which I used for the model. This data was derived from unpublished temperature records supplied by the project meteorologist, Dr. G. Courtin. Appendix 8.D.I lists the respiration "a"'s at 12 C, the degree day rate changes of respiration at 7 and 2 C, and the mean T(ime) values, which I computed from Procter (1977a). Developmental rates, and energy flows, computed by the model at 12 C, were corrected to their mean T(ime) values. Thus, developmental rates and energy flows are based on the mean of the respiration rates at 12, 7, and 2 C.

6.2.1 Rotifera

The rotifer energy flow estimate is arbitrary, since most of its parameters are arbitrary. The treatise by Donner (1966) on Rotifera was helpful, but most of the parameters used to estimate their energy flow were compiled from other invertebrate values given here. Counts of these animals were highly inefficient. I estimated the actual meadow population to be 20-fold greater than what was found. Still, their minute size and low numbers, makes their energy flow almost negligible. The raised beach population presumably undergoes cryobiosis during much of the summer. Their impact here is estimated to be negligible.

6.2.2 Enchytraeidae

The Enchytraeidae have the highest biomass, and are among the most abundant of Truelove invertebrates. They are numerically exceeded by Protozoa and Nematoda, and exceeded in biomass by

Nematoda on the raised beach (Procter, 1977b).

Cummins and Wuycheck (1971) reported that enchytraeids are $5.628 \text{ cal mg}^{-1}$ ash free, and are 9.6% ash: thus, they are $5.135 \text{ cal mg}^{-1}$. A similar value can be computed from Willard (1973c), who reported $6.091 \text{ cal mg}^{-1}$ ash free. Respiration values were calculated from O'Connor (1971). Because enchytraeids ingest large quantities of soil to digest comparatively small amounts of nutrients, their energy expenditures will be higher than those of animals consuming more digestible food. Therefore, their R/P ratio was assumed to be 1.0, double the 0.5 I used for most other invertebrates.

The maximum and minimum enchytraeid weights found in the field were used for the model weight range. The weight ranges for fragmenting enchytraeids - if they occur at Truelove - will be close enough to this 20-fold range that they will have little effect on the final energy flow values.

Three sources of biological data on enchytraeids are contradictory (Reynoldson, 1939, 1943; Ivleyva, 1953, discussed by O'Connor, 1967; and Learner, 1972). For 2 species, Reynoldson had mean values of 10 viable eggs produced per adult worm (enchytraeids are hermaphroditic). The average adult lived 0.35 the timespan required to reach maturity. When (as with the model) the survival rate of 1.2 adults declining to 0.5 (below which death occurs) lies on the same mortality curve as a 10 immatures to 1.2 adults survival rate, adults will live 0.46 of the maturation time. Ivleyva reported that enchytraeids produced 260 eggs per adult worm, and that these adults lived 12.5 times longer than the time spent as immatures. For this

to be correct, the earth should be an ever expanding mass of enchytraeids. Alternatively, for the population to be in equilibrium the survivorship of immatures must drastically differ from that of adults. Since immatures and adults are similarly shaped, live in the same habitat, and consume the same resources, their mortality curves should be similar. The data of Learner must suffer the same criticism. Both are laboratory studies which indicate the increase potential of enchytraeids, but not the actual mechanics of a field population. The field study parameters reported by Reynoldson were used in the model.

The model predicted an enchytraeid mean weight of 20.4 μg , and a maximum lifespan of 1100 C degree days. The mean weights actually collected were 20.7 μg at the raised beach and 21.2 μg at the meadow. The enchytraeids in Reynoldson's study required approximately 1100 C degree days (above 0 C) for a complete lifespan. Thus, these 2 model predictions are independently supported.

6.2.3 Tardigrada

Tardigrade biological information is from Hallas and Yeates (1972), who found that 5.4% of the parthenogenic females (no males) in their study contained 1-7 eggs. From this source, a synthetic cohort was assumed to consist of 24 hatchlings maturing to 3 pre-adults. The weight range for the model is the maximum weight difference found with Truelove specimens. It is 0.67 the range reported by Hallas and Yeates, for several species. Enchytraeid respiration rates were used for this group, while the 5.8 cal mg^{-1} and $R/P = 0.5$ were assumed values.

Tardigrades were abundant at both the raised beach and meadow sites. I suspect that they were inactive - in a cryptobiotic state - during the dry periods on the raised beach, but were rehydrated and extracted in the O'Connor funnels. If this is true, then their energy flow on the raised beach, estimated with temperature as the only driving variable, is high. I found no means to determine their actual active season.

6.2.4 Crustacea

Crustacea, found only in the meadow, were lumped into 2 groups. The Calanoidea and Cyclopoidea were combined into cohorts with a 200-fold weight range, and a decline from 100 hatchlings to 4 adults. The second group was the smaller Harpacticoidea, which have a 50-fold weight range, and decline from 18 hatchlings to 3 adults in a cohort. These ranges are from adult weights, and field estimates of egg numbers. The total egg mass was 33% of W_f , the mean adult mass. The adult weights are from a population subsample from the August 4, 1972 encytraeid funnel extractions. These weights are given in brackets (as are all subsample, or estimated, weights) in Appendix 8. The adult lifespan was assumed to be one season, based on finding reproductive adults at spring thaw which survived all summer in culture. The caloric content, 5.35 cal mg^{-1} , is the mean crustacean value calculated from Cummins and Wuychek (1971). The R/P for the crustacean *Daphnia pulex* Leydig varied from 0.37 - 32., depending on whether individuals were reproducing, and secondarily on food concentrations (from Richman, 1958). The R/P for actively

reproducing *D. pulex* was 0.48. My assumed R/P was 0.5 for growing immatures.

The "a" value of the Crustacea at 12 C was 4.869 (mean, calculated from Procter), and is the highest of all the Truelove invertebrates. Computing from Roff (1973), *Limnocalanus macrurus* Sars at Char Lake (same latitude as Truelove) has an "a" value of 4.62 at 12 C; this species matures in 9 months in its lake habitat. Comita's (1968) data for 5 arctic *Diaptomus* species, including *D. arcticus*, gives a calculated "a" of 6.6 at 12 C. Procter's high "a" value predicts maturation times of 1.08 seasons for calanoids, and 0.55 seasons for harpacticoids, which are comparatively rapid rates for these large invertebrates. This is consistent with the observed one season maturation rate of the crustaceans *Lepidurus arcticus* Pallas and *Branchinecta paludosa* (Mueller) in Truelove lakes.

Since eggs were observed only during the thaw period, I assumed that both the calanoids and harpacticoids grew during their first season, and reproduced in the second. This gives calanoids a comparatively short adult life, versus 1.45 seasons for adult harpacticoids. Because of this, in a complete lifespan harpacticoids respire a higher proportion of their energy than other Truelove invertebrates. These animals appear to be almost continually active swimmers, which implies such a high energy loss rate. Most of this energy is respired by the long-lived adults, which maintain the high "a" of the immatures, without growing. The Calanoid respiration energy loss was proportionately less, because there were immatures in a

cohort, and some maturation occurred during the second season.

6.2.5 Acarina

The Truelove soil Acarina were oribatids. Wallwork (1967), and Block's (1965) study of the life histories of 2 soil dwelling oribatids, especially *Damaeus clavipes* (Hermann), are the main information sources for the Acarina synthetic cohort data. A cohort consists of 60 hatchlings maturing to 6 adults; the immature weight range is 30-fold. The weight specific respiration rates, for the 2 Truelove oribatid species, were the lowest for all invertebrates measured by Procter, and give the lowest computed "a" value, 0.5621. Cummins and Wuycheck list $5.808 \text{ cal mg}^{-1}$ for Acaridae, which are lightly sclerotized. I estimate the more heavily sclerotized oribatids to be 5.5 cal mg^{-1} . The R/P ratio was assumed to be 0.5 for immatures.

The model predicts that Acarina require 2.6 years to mature on the raised beach, and 5 years on the meadow. The last individual in a cohort dies in 11-fold this maturation time.

The Acarina populations have one astonishing feature. Wallwork (1967), working with a Michigan forest soil population, found that 50% of the mites he extracted were adults, and 50% immatures. Addison (pers. comm.) found the same age distribution at the raised beach, where 50% of the 1972 and 53% (572 unsclerotized/651 sclerotized) of the 1973 Acarina were heavily sclerotized (= adult). To maintain the 50:50 ratio, with the same exponential mortality rate for both adults and immatures in a cohort with 60 starting individuals, the average adult must live 11-fold as long as the average immature. This is true

regardless of the number surviving to adulthood. Thus, some individual mites will live up to 29 years on the raised beach, and up to 55 years in the meadow. If cohorts were numerically smaller, this timespan ratio would be reduced, but the adult lifespan would still be many-fold the immature lifespan.

This long lifespan prediction could be based on a faulty assumption. Adults and immatures, because they differ in body form, ought to have different mortality rates. The adult mortality rate might be drastically reduced, compared to that of immatures, until old age death. Then, it must become precipitous when adults get senile. This would not require such long adult lifespans.

Long adult lifespans, or strikingly different adult mortality rates, are the 2 choices apparent for allowing the 50:50 ratios observed. (A third choice, that immatures are less efficiently extracted than adults by these Macfadyen Hi-Gradient extractors, would necessitate a completely speculative revision of this information). Long mite lifespans have been noted in temperate areas (cf. Wallwork, 1967). Englemann (1961) reported that 96% of the energy assimilated by his oribatid populations was respired, which necessitates that growing immatures were a small segment of these populations. Since this evidence supports the original conclusion, I shall leave this information as stated, with the 29-55 year lifespan prediction as a testable hypothesis generated by the model. An acarologist, R.W. Strandtmann (e.g. Strandtmann, 1971), intends to consider this hypothesis in 1977 on Ellef Ringnes Island.

6.2.6 Araneida

There are 2 natural divisions of the spiders at Truelove, the larger lycosid *Tarentula exasperans* P.-C., and the small linyphiids and rare dyctinids. A *T. exasperans* cohort has 70 hatchlings, which produce 5 adults, while a linyphiid cohort has 16 hatchlings, producing 3 adults (Leech, 1966, and pers. comm.). Adults die the same year they produce eggs. The weight ranges of 100-fold for *T. exasperans*, and 75-fold for linyphiids, are based on adult weights, egg numbers, and estimated and measured egg sac weights. The respiration "a" value for an arctic *Lycosa* sp. (Scholander *et al* 1953) was used for both cohort groups. Data in Moulder *et al* (1970), and additionally from Riegert *et al* (1974), indicates that tissues are 5.8 cal mg^{-1} , and suggests that the lifespan R/P should be 1.7. I compromised this using immature R/P's at 1.4, which determines the lifespan values to be 1.42 and 1.46. As the immature R/P increases, the adult contribution to respiration decreases proportionally, to a degree that is inconsistent with the patterns of other invertebrates. Edgar (1971b) reported a lifespan R/P of 2.5 for *Pardosa (Lycosa) lugubris* Walc., which would lengthen the spider lifespans by 150% of that reported here. I used the lower R/P to minimize the required developmental time.

The model predicts that *T. exasperans* cohorts mature in 8 years on the raised beach, and the smaller linyphiids require 9 years at the meadow. Both spend an additional year as adults. The mean weight of *T. exasperans* collected is predicted to be 4.4 mg, while the actual

mean weight collected was 17.5 mg. Because of this, I increased the lycosid energy flow by $3.95 = (17.5/4.4)$. Similarly, linyphiid energy flow was increased by the 597 μ g collected over 113 μ g predicted means.

The 8 year maturation period predicted for lycosids is close to the 6 year maturation period postulated for lycosids at slightly warmer Lake Hazen (Leech, 1966). No times are available for linyphiid comparisons. It is probably incorrect (cf. Appendix 2) to use temperatures at -1 cm for the activity season of these animals, but I have no alternate base temperatures for them. Two factors in the spider energy budgets require explanation. The first is that the predicted *T. exasperans* mean weight is 0.25 the collected mean weight. This requires that survival to maturity is greater than was assumed, or that the sampling technique favored the collection of mature specimens. Both alternatives may be correct, and both indicate that the present model values underestimate the actual energy flow. Therefore, I increased the model energy flow by (observed/predicted weights) = 3.95-fold for *T. exasperans*, and by 5.29-fold for the linyphiids.

Despite this corrective increase, the spider energy flow is comparatively low. Researchers at other sites have ascribed to spiders a proportionately larger (Heal *et al*, 1975) to much greater (Danilov, 1972; Mani, 1968) role than was found here. The Lowland apparently is less favorable to, or less colonized by, spiders. Illusion may also be involved. Active predators are disproportionately collected with respect to their potential prey, creating an inflated

impression of their importance (Southwood, 1966). Incomplete "methods" sections in Danilov and Mani, and apparently excessive claims of spider importance (e.g. Danilov reported that 56% of all arthropods were predators, mostly spiders), leads me to suspect that both workers used relative abundance sampling techniques. Pitfall trapping at Truelove yielded 460 spiders/trap in a season, but absolute sampling techniques showed the standing crop to be 0.3 individuals m^{-2} on the raised beach, and 1.8 m^{-2} on the meadow.

The raised beach spider (= *T. exasperans*) corrected energy flow was 63 cal m^{-2} , while the emergence trap insect catch was 53 cal m^{-2} . Allowing additionally that the winged insects metabolize and oviposit part of their "trap collected" mass before death, and that spiders do not totally consume their prey, appears to make the spiders more than 100% efficient in capturing the raised beach Diptera adults. Sweep net samples showed that swarms of Diptera frequently flew above the raised beaches, creating an impression that the raised beaches produced more Diptera than meadows. Actually, Diptera from adjacent meadows and water bodies had swarmed over the raised beaches. Once there, they were available for consumption by spiders. A similar migration may explain Kajak's (1971) otherwise unconvincing report that spiders consumed the entire winged insect emergence of her study area. The Truelove spiders have a comparatively low energy flow, but this quantity is sandwiched within known parameters of food availability.

6.2.7 Collembola

Collembola at Truelove were investigated by Addison (1977),

who found *Hypogastrura tullbergi* (Schaeffer) to be dominant on the raised beach. Individuals of this species survived 2-3 years beyond the 1-2 year maturation period on the raised beach site. Hale (1967) reported that, under sub-arctic conditions, probably fewer than 100 eggs are laid by most species of Collembola during the lifetime of a single female. For the model, a cohort starts with 60 hatchlings. Since both juveniles and adults are similarly shaped, moult continuously, live in the same habitat, and consume the same food, mortality rates should be similar for all stages. From Addison's study, it is also known that adults survive 50% longer than the required maturation time. These 2 factors determine that 8.7 adults are produced in a cohort of 60 hatchlings. The weight range I measured at Truelove, 28-fold, was used for the model. The values 5.8 cal mg^{-1} and R/P ratio of 0.5 for immatures are both assumptions.

The model predicts a 1.25 year maturation period, and a 1.9 year adult lifespan, for Collembola on the raised beach. On the meadow, a 2.4 year maturation period, and a 3.7 year adult lifespan, are predicted. The population mean weight predicted was 4.8 ug , versus 4.9 ug actually collected, at the meadow, and 5.2 ug versus 5.3 ug collected, at the raised beach. The predicted maturation period on the raised beach compares favorably to Addison's conclusions of 1-2 years. This suggests that the assumed R/P value is approximately correct, as is the weight range.

I suspect that even the Macfadyen high gradient apparatus favors the extraction of bigger individuals in a population. Hence, the actual Truelove Collembola populations are probably larger than

the uncorrected values reported here. This means that the total Collembola energy flow should be somewhat greater. I did not operate the Macfadyen apparatus myself, however, and Addison made no extraction efficiency tests, so I shall leave these results as presented.

6.2.8 Pterygota - Diptera

The pterygote insects are Diptera and Hymenoptera, and also Lepidoptera on the raised beach. All other pterygotes are rare or absent from the site. As with other invertebrates, larvae are the only pterygote insect lifestages that can be analysed by the computer model. Pupae and adults are altogether different, and require special interpretation to estimate their mortality and respiratory losses.

The numbers of synthetic cohorts m^{-2} for the model were based on the emergence trap data, and on the *Gynaephora* model (Chapter 3). These were 1/4 of the number of adults collected, except for Hymenoptera Apocrita, which was 1/32 of the number of adults collected. The final number in a developing cohort was 5, and 40 Hymenoptera Apocrita, with the differences (1, and 8 individuals) being due to mortality between the prepupal stage and captured adults. Adults at death are an estimated 67% of the mass of newly-emerged adults. The mass of each adult captured is an estimated 67% of its prepupal mass. Welch (1973) found emerging female chironomids were 40% eggs. This percent of the emergence weight of 1 of the 4 emerged adults is taken to be the initial mass of hatchlings in a cohort. The R/P ratio was assumed to be 0.5 for all pterygote larvae other than herbivores, whose R/P is 0.8. Caloric values are those measured for Truelove insects.

The weight range manipulations for pterygote insects have a simple logic. Insects collected in emergence traps were not at their maximum emergence mass. The trap vacuuming procedure (5.2.1.3.2) indicated that they remained in these traps up to several days before being captured. From the stage when feeding ceased, the prepupa, to the captured adult, individuals lost weight by metamorphosing and flight metabolism, by moulting twice, excreting a meconium, and by depositing eggs. Leaching into the alcohol preservative is another source of weight loss (Dermott and Patterson, 1973). The sum of these losses was estimated to be 33% of the prepupal mass at the time the adult was trapped. The weight at adult death, estimated from the blowfly weight loss experiment (Table 13) and from the loss of egg mass, was 67% of the estimated weight at emergence. This recognizes the probability that adults in the field do not die of total exhaustion, but are killed by weather or predators when their body reserves are partially depleted.

Diptera were treated as 4 cohort units in this analysis. The first is chironomids and sciarids (96% chironomids), which are similar-sized nematoceros Diptera. Oliver (1968) found a mean fecundity of 160 eggs for several arctic chironomid species, while Welch (1973) found 160-212 for 4 species. The mean fertility of females in this group is taken to be 160 hatchlings for the synthetic cohort. The respiration "a" value, a mean from 4 chironomid species, was used for these cohorts, and for the other 2 nematocera groups. These 2 groups, Mycetophilidae from the meadow site, and Tipuloidea from the raised beach, are assumed to have the same reproductive capacities as the first group. The fourth group is primarily Muscidae

and Anthomyiidae, but includes the occasional empidid, dolichopodid, and syrphid. Extrapolating from Buei's (1967) laboratory fecundity studies with *Musca domestica* Macq. to field conditions, I estimate that flies in these cohorts have 80 hatchlings. *Protophormia terrae-novae* caloric values can be variable, but are highest (5.4 - 5.7 cal mg^{-1} reported) in flies reared in cold environments (Hoffmann, 1976). I used 5.8 cal mg^{-1} , as measured at Truelove.

Raised beach chironomid and sciarid larvae are predicted to require a 0.9 year maturation period, while Tipuloidea and Cyclorrapha require 1.6 and 1.9 years, respectively. At the meadow site, chironomid and sciarid larvae require a 1.8 year maturation period, Mycetophilidae require 2.3 years, and Cyclorrapha require 4.4 years. Pupal and adult lifespans were not predicted.

The predicted chironomid and sciarid maturation times in the meadow are equivalent to known arctic lake chironomid maturation times of 2-3 years (Oliver, 1968; Welch, 1973), while those on the raised beach are markedly shorter. The Tipuloidea include trichocerids, which mature in 1.2 years, and tipulids, which require 2. This latter time is equivalent to the 4 years required by the tipulid *Pedicia hanna* in colder meadows at Pt. Barrow (MacLean, 1973). Tipuloid adults were collected only from the raised beach site, while tipuloid larvae were found only at the meadow by the regular soil sampling program. These insects were contagiously distributed, with low numbers. Only a raised beach energy flow value is presented here, because all pterygote insect results are based on emergence trap adult catches. The Cyclorrapha energy flows can be computed through the respiration rates of either Procter or Scholander *et al.*

Scholander's rates give 12% faster maturation times.

The model predicted mean larval weights, and the weights found by soil sampling, correspond poorly. Very few tipuloid and cylorraphan larvae were collected by soil sampling, and these were usually large individuals. For the chironomids -plus, the predicted mean individual weights were 8-24% of those collected. The predicted larval population numbers (not given here) are also several-fold those found, despite the correction factor increases. When the model predicts larger populations of smaller individuals than are actually found, some of the difference can be attributed to extraction efficiencies, as extraction and counting procedures favor the recovery of larger individuals. The corrected standing crop biomasses are approximately the same as those predicted. Also, these predicted populations are based on a single season's emergence, yet an individual lifespan can be many years. This complication means that there are overlaps of many years' cohorts. Predictions about a single year's population have limited meaning without several years of extraction results. This can be true for all long lifespan invertebrates.

If the initial number of hatchlings in a cohort were less, or the final numbers greater, the predicted mean weights and population numbers would be closer to those actually found. The literature cited as the source for the values used, my lack of fecundity measurements for Truelove Diptera, and the *Gynaephora* model, prevent making any such changes without further study. The total Diptera energy flow would be less than, but still close to, the present values if I made the input value changes necessary to predict lower larval populations with higher individual biomasses.

6.2.9 Pterygota - Lepidoptera and Hymenoptera

Lepidoptera, and Hymenoptera Symphyta, both being herbivorous pterygotes, were assumed to have the same fecundity, 100 offspring per female. Hymenoptera Apocrita parameters are also assumed, with 60 hatchlings declining to 40 in a cohort, and $R/P = 0.5$ since they are carnivores. The respiration "a" of *Gynaephora* was used for the Lepidoptera and Hymenoptera Symphyta, while the mean chironomid "a" was used for Hymenoptera Apocrita (=parasitica).

Only one Lepidoptera adult was captured in the emergence traps, on the raised beach. The model predicts it required 3 years to develop. Hymenoptera Symphyta require 3 years on the raised beach, and 5 years on the meadow, to mature. Parasitic Hymenoptera require 1.2 years on the raised beach, and 2.4 years on the meadow, to mature.

Both groups are minor energy releasers. The input values for the model, particularly the number of offspring, are tentative. I observed that one field-collected *Psychophora sabini* female (specimen collected in the emergence trap) laid approximately 25 eggs. The egg laying habits of sawflies are markedly different from *Gynaephora*'s, and I believe that their reproductive output is less than *Gynaephora*'s 160 eggs per female. Lacking adequate specific information, I assumed that these reproducing females deposited 100 viable eggs. The Lepidoptera energy flow of 31.5 cal m^{-2} compares well with the 3.3 cal m^{-2} predicted for *Gynaephora* alone. *Gynaephora* were rare, so they had proportionally less impact. Some discrepancy is attributable to the low sample numbers, i.e. 3 *Gynaephora* collected in all the *Gynaephora* sampling, and 1 lepidopteran collected in 2 years of emergence trapping.

From field observations on the abundance of Lepidoptera, I suspect that the emergence trap energy flow prediction is closer to being correct.

The Hymenoptera parasitica cohort numbers were based on counts of the number of adult *Apanteles* sp. emerged from 6 cocoons. A mean of 29 adults emerged from 32-34 pupae. I substituted 32 adults from 40 pupae, per parasitized host, for the model. Parasites are unique in their high percentage of successful development to adulthood within a host, and the need for a large number of adults to find hosts for the next generation. The large number of adults produced in a cohort, versus the low number of larval deaths, means that adults respire a higher portion of the energy lost. This gives these populations a higher R/P than for other invertebrates.

6.3 Energy Flow Through Truelove Invertebrates

Energy flows through Truelove invertebrates (excluding nematodes) are shown in Table 15 (except Protozoa, given in Table 14). Figure 9 is a diagrammatic presentation of Tables 14-16 data. Energy flows are given as mg of tissue produced, and ml of O_2 consumed, and their respective conversions to Joules. Table 15 results are the conclusions from Appendix 8 data. They are based on 1972 population figures, and on seasonal mean temperatures from 1971-73. I can not offer probable error ranges for any Table 15 data. Comparisons of model predictions and field data, and comparisons for self-consistency, and consistency with known ecosystem inputs, are the only checks on these data. None of these checks conflict.

At the meadow site, the Protozoa are dominant, with an assimilation of $105 \text{ KJ m}^{-2} \text{ yr}^{-1}$. The enchytraeids rank second at 30 KJ

Table 15. Invertebrate energy flows on the Truelove Lowland

Taxon	Site	$\text{mg m}^{-2} \text{yr}^{-1}$ Produced	$\text{ml m}^{-2} \text{yr}^{-1}$ Respired	Joules $\text{m}^{-2} \text{yr}^{-1}$ Produced	Joules $\text{m}^{-2} \text{yr}^{-1}$ Respired
Protozoa	M	1440	3560	35000	70000
Rotifera	M	1.089	0.949	26.43	18.66
"	R b	0.0748	0.065	1.82	1.28
Enchytraeidae	M	584	895	12500	17600
"	R b	412	631	8850	12400
Tardigrada	M	4.41	3.61	107	71
"	R b	14.2	11.7	346	229
Crustacea					
Calanoidea-plus	M	35.1	29.7	786	584
Harpacticoidea	M	13.4	34.0	299	668
Acarina	M	1.28	3.26	29.6	64.2
"	R b	3.53	9.01	81.3	177
Araneida					
Linyphiidae	M	0.769	1.39	18.7	27.4
<i>T. exasperans</i>	R b	4.49	7.86	109	155
Collembola	M	32.5	30.8	789	606
"	R b	145	137	3520	2700
Lepidoptera	R b	2.14	3.97	51.9	78.1
Diptera					
Chironomidae-plus	M	103	132	2500	2600
Mycetophilidae	M	0.813	1.04	19.7	20.5
Cyclorhapha-plus	M	51.2	71.0	1240	1400
Tipuloidea	R b	5.55	7.10	135	140
Chironomidae-plus	R b	10.1	12.9	244	253
Cyclorhapha-plus	R b	6.81	9.43	165	185
Hymenoptera					
Symphyta	M	2.05	3.81	49.8	75.0
"	R b	1.69	3.14	41.0	61.7
Apocrita	M	0.625	1.65	15.2	32.4
"	R b	0.389	1.03	9.44	20.3
Summary:					
all Inverts.	M	2270	4640	53400	91200
all, excl. Protoz.	M	830	1080	18400	21200
"	R b	606	743	13500	14600
Insects only	M	190	240	4620	4730
"	R b	171	175	4160	3440

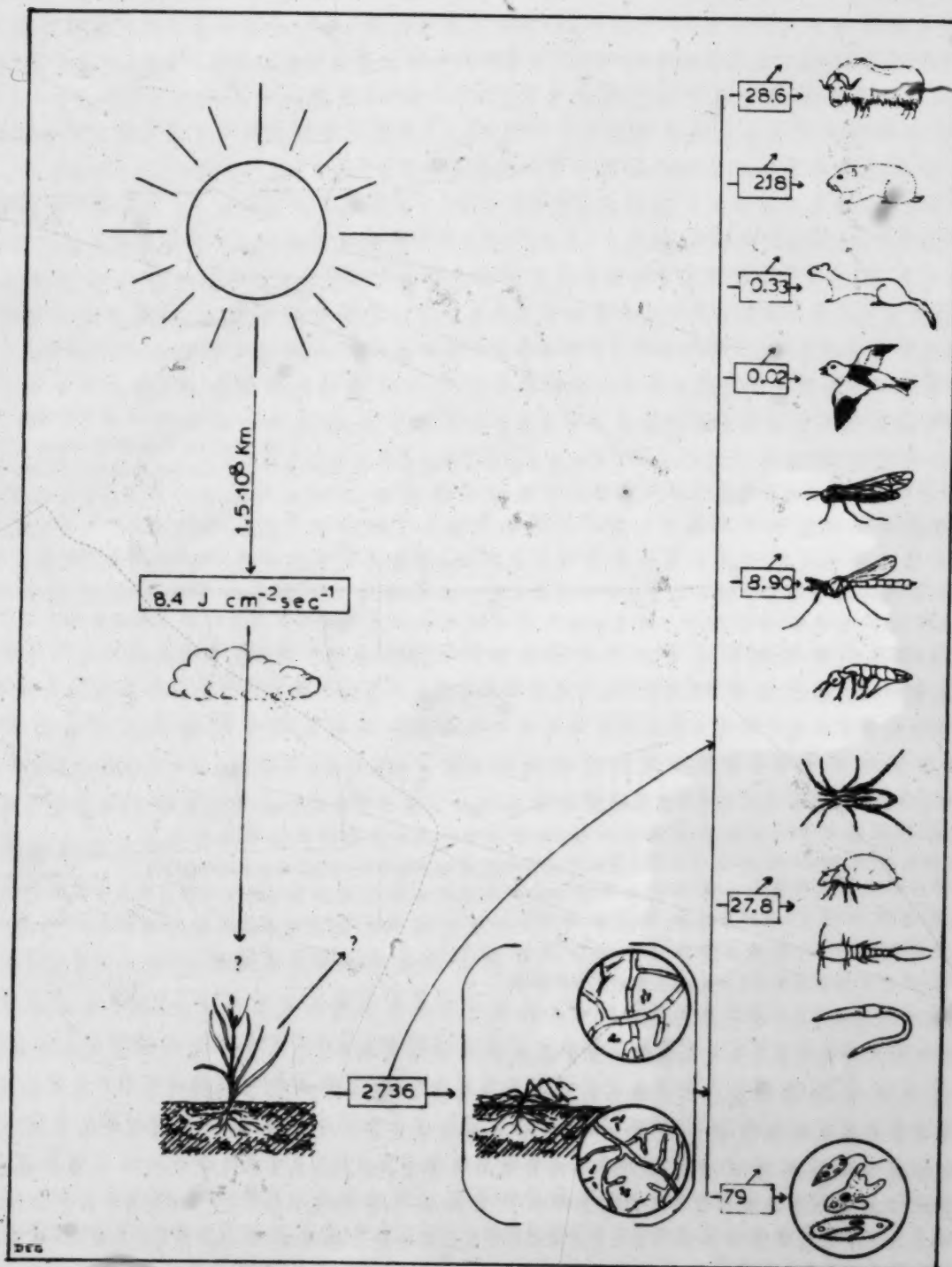


Fig. 9. Pictorial summary of energy flow. A. Energy assimilated (KJ m⁻²yr⁻¹) at the Truelove Lowland.

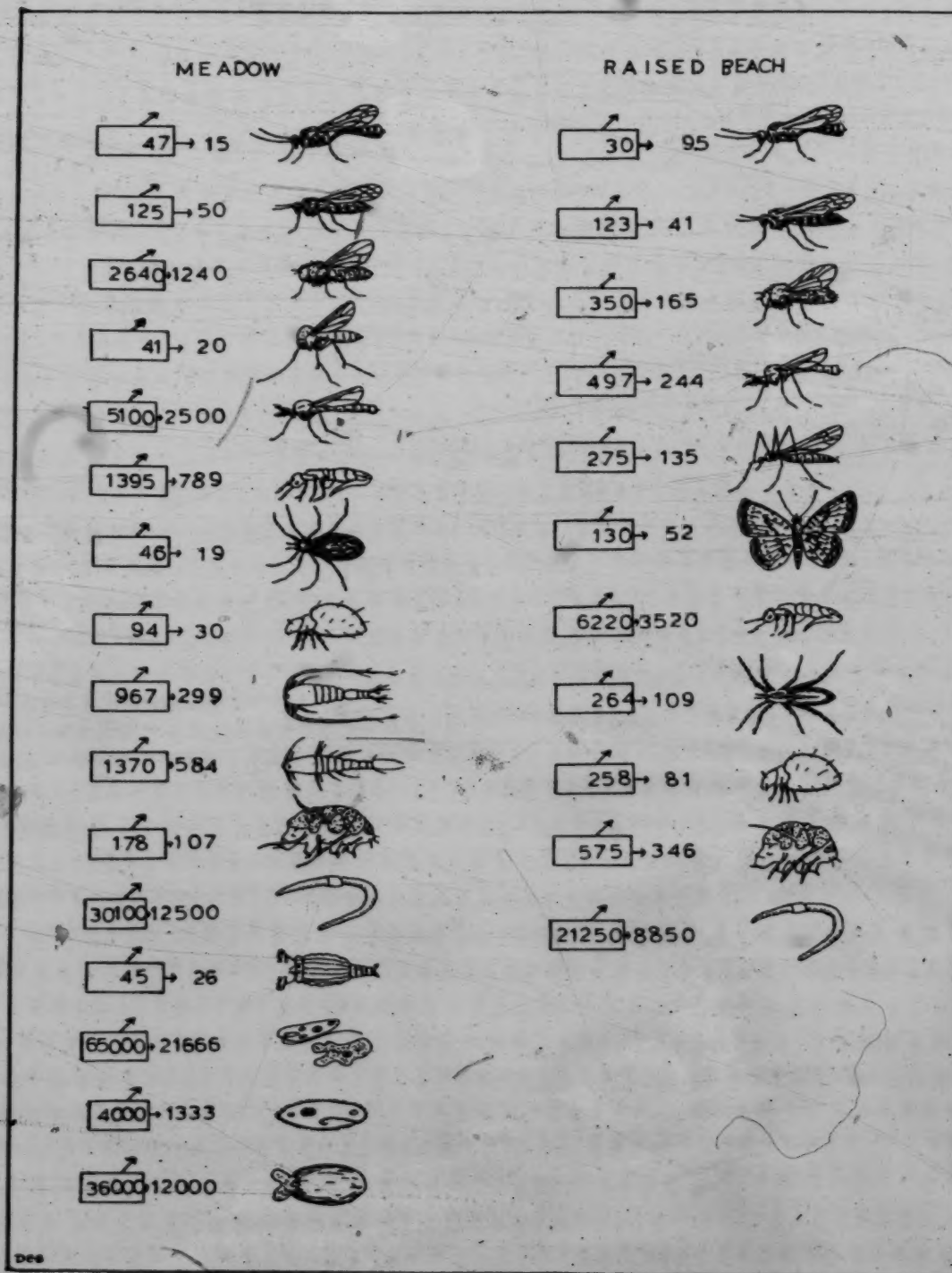


Fig. 9 (con't) B. Assimilation, production and respiration ($\text{J m}^{-2}\text{yr}^{-1}$) of Invertebrates.



C. Diagram of production and respiration for a *Gymnophora* sp. cohort.

assimilated $\text{m}^{-2} \text{yr}^{-1}$. Flies are third in significance, with chironomids and sciarids assimilating 5.1 KJ, and cyclorrapha-plus assimilating 2.6 KJ. The combined crustacean assimilation is 2.3 KJ. Collembola assimilate 1.4 KJ, and are the last group to assimilate more than $1 \text{ KJ m}^{-2} \text{yr}^{-1}$. Tardigrades, Acarina, and Hymenoptera Symphyta each assimilate approximately 0.1 KJ. Rotifers, Araneida, mycetophilids, and Hymenoptera Apocrita, at less than $0.1 \text{ KJ m}^{-2} \text{yr}^{-1}$, are negligible energy assimilators. No Coleoptera or Lepidoptera were found at this site.

On the raised beach, the enchytraeids are the dominant group at $21.3 \text{ KJ m}^{-2} \text{yr}^{-1}$ assimilated. Collembola rank second at 6.2 KJ. Other invertebrates are all below $1.0 \text{ KJ m}^{-2} \text{yr}^{-1}$. In ranked order, these are the tardigrades, at 0.58 KJ, chironomids and sciarids at 0.50 KJ, cyclorrapha-plus at 0.35 KJ, tipuloids at 0.27 KJ, Acarina and *Tarentula exasperans*, both at 0.26 KJ, Lepidoptera at 0.13 KJ, and Hymenoptera Symphyta at $0.10 \text{ KJ m}^{-2} \text{yr}^{-1}$. The Rotifera, Mycetophilidae, and Hymenoptera Apocrita combined assimilate less than $0.1 \text{ KJ m}^{-2} \text{yr}^{-1}$. The impact of Protozoa was not estimated, but is certainly much less than their impact at the meadow. Nematode populations are large (c.a. $4 \cdot 10^6 \text{ m}^{-2}$) at the raised beach (Procter, 1977b), so they are an important energy flow component which is not included in this summary. No Coleoptera were collected in population sampling at the raised beach, although *Amara alpina* Paykull has been found at the site.

6.4 Energy Flow Through the Ecosystem

How does invertebrate energy flow compare to other energy flows in this ecosystem? Because the vertebrates range widely over

the Lowland, this question cannot be answered directly for either study site. The vertebrate impacts on the lowland plant communities have been assessed (c.f. Whitfield, (1977), and the vertebrate papers in Bliss (1977)).

By assuming that the vertebrates have the same impact on the study sites as they have on similar lowland sites, comparisons can be made. The net primary production at both study sites is known (Bliss, 1975). Hummocky sedge moss meadows, like the intensive study meadow, cover 20.6% of the Lowland, while cushion plant lichen communities, as the raised beach site, cover 6.8%. This data can be combined to make an artificial community which represents 27.4% of the lowland area.

The results of these combinations are shown in Table 16, in $\text{KJ m}^{-2} \text{yr}^{-1}$. Muskozen were the dominant vertebrates by a 10-fold margin. The combined invertebrate (excluding nematodes) assimilation, 116 KJ, was 3.7-fold the combined vertebrate energy assimilated. Altogether, the secondary producers of this ecosystem assimilated 5.4% of the net primary production. The insects accounted for 24% of the total invertebrate (excluding Protozoa and nematodes) energy assimilated, and assimilated 29% of the amount which the combined vertebrates assimilated.

Although these values are tentative, they are sufficient to indicate the relative energetic importance of invertebrates. In this cold-dominated ecosystem, where they are inactive 10 months yr^{-1} , the invertebrates are the major animal energy releasers by a several fold margin.

A major difference between invertebrates and warm blooded

Table 16. Comparative summary of energy flows on the Truelove Lowland.

	<u>Kilojoules m⁻² yr⁻¹</u>
Net Primary Production	2736
Assimilation:	
Muskox	28.6
Lemming	2.18
Birds (excluding carnivores)	0.02
Vertebrate carnivores	0.33
All Invertebrates	115.7
Invertebrates (excluding Protozoa)	36.7
Insects	8.90
<u>Ratios</u>	<u>Percentages</u>
Protozoa/Meadow N.P.P.	3.0
Invertebrates/N.P.P.	4.2
Secondary Producer Assimilation/N.P.P.	5.4
Invertebrates/Vertebrates	370.
Insects/N.P.P.	0.33
Insects/Invertebrates (excluding Protozoa)	24.
Insects/Vertebrates	29.

vertebrates is that the warm blooded animals metabolize a large proportion of their assimilated energies to produce heat. Therefore, from the same quantity of assimilated energy, vertebrate tissue production will be less than invertebrate production. Most of the assimilated vertebrate energy is respired, while a distinctly larger proportion of the invertebrate tissue energy remains as produced tissue, available for further passage through the ecosystem.

6.5 On the Structure of This and Other, Ecosystems

Severe cold has retarded the rate, and reduced the complexity, and number, of biological interactions on the Truelove Lowland. Study of this high arctic ecosystem suggested several basic concepts to me about its organization, and the structure of terrestrial ecosystems in general. In the *Gynaephora* chapter (3.10) I discussed the impact of invertebrate herbivores in several ecosystems, and proposed that 1) generally, herbivores assimilate only a small percentage of the net primary production, and 2) that there is a latitudinal gradient to invertebrate herbivory, with the highest percent of N.P.P. being assimilated in temperate climates. Two other ecological concepts will be discussed in this section.

Most energy release occurs in the soil. Protozoa, Nematoda (not discussed here - see Procter, 1977b), Enchytraeidae, Acarina, Collembola, and Diptera larvae are all soil dwellers, and the major invertebrate energy releasers. Activity above the soil surface, although it is more obvious, is minor in comparison. Fungi (Widden, 1977) and bacteria (Nelson, 1977), the major energy releasers of this ecosystem, are also soil organisms, as most are found in, or on the surface of, soil. Thus, while energy fixation occurs in plant

leaves above the soil surface, the greatest conversion and release of energy occurs in, and at the surface of, soil.

The feeding habits of these invertebrates must be determined primarily from literature sources (c.f. especially Burges and Raw, 1967). Lepidoptera and Hymenoptera Symphyta are herbivores, as are some small portion of the Nematoda, Acarina, Collembola, Diptera, and Hymenoptera Apocrita. Herbivory is a minor component of the True-love energy flow.

Carnivory is characteristic for all Araneida, and for some portion of the Protozoa, Nematoda, Tardigrada, Crustacea, Acarina, Collembola, Diptera, and Hymenoptera Apocrita. This energy pathway is more important than herbivory, but is still comparatively small. Allowing for capture inefficiency, and other causes of death, carnivory potential in a closed ecosystem is necessarily much less than the net production of prey organisms.

The pattern of energy flow in this ecosystem is dominated by the detritus food chain. Bacteria, fungi, and partially decomposed organic matter predominate in the diets of Protozoa (Stout and Heal, 1967); Rotifera (Pennak, 1953); Nematoda (Nielsen, 1967); Enchytraeidae (O'Conner, 1967; Dash and Cragg, 1972); Tardigrada (Hallas and Yeates, 1972); Crustacea (Pennak, 1953; Bottrell, 1975); Acarina (Wallwork, 1967; Luxton, 1972); Collembola (Hale, 1967); and Diptera (c.f. Stone *et al* 1965, Dowding, 1967). When these taxa, and other detritivores, are dominant in other ecosystems, the basic pattern of invertebrate energy flow in these ecosystems will be through decomposition. Most natural ecosystems appear to be decomposition based, from an invertebrate viewpoint (e.g. Fittkau and

Klinge, 1973 for tropics, Willard 1973d for grassland, Bottrell, 1973 for freshwaters, Steele, 1970 for marine environments, and results of current IBP studies).

Why do the bulk of invertebrates remove themselves one trophic level from the primary food source? Few invertebrates possess cellulase enzymes (known from Protozoa, annelids, nematodes, snails, beetles, tipulids, and possibly Thysanura) (Bjarnov, 1972; Edwards *et al* 1970; Gascoigne and Gascoigne, 1960; Lasker and Giese, 1956; Nielsen, 1962; Zinkler, 1970). Given the abundance of cellulose in ecosystems, and the complexity of enzyme systems in all animals, cellulases would be comparatively simple to produce. Why, then, are they rare?

The answers lie in studies of ruminant metabolism (Briggs, 1967; Dougherty, 1965). Cattle generally consume dead plant tissue of low nutritional value. This material is thoroughly masticated. Urea is added in the saliva. This mixture is incubated in a stomach with bacteria and protozoa. These microorganisms produce cellulases, degrading cellulose to waste products of acetic acid, propionic acid, methane gas, and other products. They grow on this diet, synthesizing needed vitamins, and also converting nitrogen, as in urea, to amino acids for body proteins. This mixture passes into the cow's intestine, and the cow's own digestive compounds are added. The bacterial and protozoan bodies are digested, along with their wastes, and undigested fibers are passed. Thus, the apparently herbivorous cow is in reality a saprovore, digesting bacteria, protozoa, and their metabolic wastes. Passed wastes can be recycled through the cow for further digestion. Nitrogen, as in bird guano, may be added to the fodder to enhance bacterial growth, and hence cow net production.

The advantages of this pathway to the cow are considerable:

1) production, and concentration, of protein, 2) synthesis of vitamins, and 3) degradation of cellulose to usable compounds, all by the gut fauna. Consider the basic food requirements of a mammal, then the composition of dead plant tissue. Plants consist largely of carbohydrate structure, i.e. cellulose, and have low protein content. If a cow, lacking ruminant symbionts, produced a cellulase, and ate only fodder, it would face a surfeit of carbohydrates, and deficits of protein and vitamins. Thus, cattle are confronted with a case of Liebig's Law of the Minimum. Ruminant symbiosis was evolutionarily the most efficient pathway to acquire protein, and vitamins; and excess carbohydrates are unimportant. Ruminant symbiosis has allowed vertebrates to massively invade regions where they can survive on nutritionally poor diets, the only food available for much of the year.

The same situation pertains to the invertebrates. The composition of dead plant material is radically different from the diet required by invertebrates. It is more efficient to digest bacterial and fungal biomass, and degraded plant material. Cellulose, a surplus commodity, is decomposed by bacteria and fungi in the soil (Brock, 1966; Dickinson and Pugh, 1974; Hughes and Rose, 1971; Siu, 1955). In this manner, soil invertebrates are like ruminants, but with their ruminant symbionts outside their bodies. They gain advantage from being a trophic level removed from the primary food source. Some invertebrates possess cellulases, which enable them to derive metabolic energy for maintenance or to produce usable wastes, i.e. snail's slime. But these are abnormal mechanisms, and alone will not permit growth and reproduction. Herbivorous invertebrates generally

must consume live protein, as in plant leaves, or protein rich plant tissue, such as pollen and seeds. Otherwise, they must benefit from microbial intercession.

The microbial pathway to invertebrate biomass appears to be basic to world ecosystems. It is preserved in the Arctic, and is found in tropical and temperate climates.

Chapter 7

INVERTEBRATES AT TRUELOVE LOWLAND

The composition of the Truelove Lowland invertebrate fauna was unknown at the inception of this project. Except for notes on abundant pterygote insects (Hussel, 1972), and a visit by chironomid specialist D.R. Oliver (pers. comm.), the fauna was uninvestigated. An ecosystem can be described by its components. I listed the numbers of vascular and non-vascular plant, and vertebrate, species found in the Lowland (1.1) to permit comparison with floras and faunas of other sites. To discuss energy flow through Truelove invertebrates, it is necessary to specify which invertebrates were present during this study. For simplicity, I used groupings of higher taxa in the energy flow model (Chapters 4, 6). In this Chapter I discuss the species composition of these taxa, and list all invertebrates determined from the Truelove Lowland fauna.

7.1 Polar Faunas

Invertebrate species diversity is reduced in the Arctic (MacLean, 1975). This follows logically from the reduced plant diversity (Porsild, 1964; Saville, 1972), and the consequent reduction of habitat diversity. The evolution of diversity depends primarily upon climatic stability, and time (Dobzhansky, 1950). The first arctic tundra probably appeared in the Queen Elizabeth Islands 6-8 million years ago; the first definitely determined tundra

appeared 1 million years ago (Hopkins, 1974). So tundra biota has had a comparatively brief time to evolve. The insect fauna is derived by reduction from lower latitude faunas, with limited *in situ* evolution at the species level (Downes, 1962, 1964, 1965). This reduction pattern can be seen in latitudinal diversity gradients. A classical gradient is the reduction in numbers of ant species in South America at successively higher latitudes (Darlington, 1965).

The continental antarctic fauna is extremely limited. The only insects are 7 species of Collembola (Tillbrook, 1970) and 2 of Diptera (chironomid flies) (Gressitt *et al* 1963). South Georgia, and Victoria Islands, support reduced invertebrate faunas (Collins *et al* 1975; Jenkin, 1975; Tillbrook, 1967).

Arctic regions cover extensive areas of the northern hemisphere. Much of the western European arctic corresponds to the Canadian boreal forest sub-arctic (Rosswall and Heal, 1975). Western European arctic and temperate faunas are frequently well documented for limited areas (Nelson, 1971, Luff *et al* 1974; journal, Zoology of Iceland). The USSR contains most of the palearctic true tundra. Most Russian faunal information is unavailable in English, except for specific IBP exchange information (Chernov, 1975a,b; Chernov *et al* 1975a,b). A comparison of invertebrate species lists from the IBP tundra sites ranks them on a gradient, showing that species diversity corresponds approximately to site latitude (Ryan, 1976).

In the US Arctic, the arthropod species list for Pt. Barrow, Alaska, compiled initially by Hurd and Linquist (1958), and expanded by Bohnsack (1968) and Challet and Bonsack (1968), is commendably thorough. Nematodes, oligochaetes, and other invertebrates are

currently being added to this list (MacLean, pers. comm.). The Report of the Canadian Arctic Expedition, 1913-18, vol. 3, 7, 8, are comprehensive for all invertebrates, but this expedition did not explore high arctic areas. The Lake Hazen lists of Insecta (Oliver, 1963), Nematoda (Mulvey, 1963), and Araneida (Leech, 1966), with additions (Richards, 1963, 1964; Kevan, 1970), make this the best documented high arctic fauna. McAlpine (1964) listed insects collected in the Queen Elizabeth Islands, and at exceptionally depauperate Ellef Ringnes Island (1965). A Bathurst Island arthropod fauna list was compiled by Danks and Byers (1972).

7.2 Methods

Specimens were purposely collected for determination from 1970-74, the duration of this project. Collecting procedures included sweep netting, pitfall trapping, hand collecting, malaise trapping, and soil extracting. This species list includes material collected and determined by other IBP researchers, but the majority of determinations were made through my efforts. It is comprehensive, except for Nematoda, which will be treated by Procter (thesis in prep.). Specimens of every taxon listed here were sent to one or more experts, but not all were returned with determinations. The determining authority for each taxon is included on the list. I have separated it into sections for presentation and discussion.

7.3 Results

The Protozoa list (Table 17.A) was compiled during the August 5, 1972, examination of meadow soil Protozoa by Dr. O.W. Heal (Chapter 6.1). His comment on the protozoan fauna, preceding

Table 17. Invertebrates at Truelove Lowland. A. Protozoa

Taxon	Determined by
Kingdom Animalia	
Subkingdom Protozoa	
Phylum Protozoa	
"It can be said that the protozoan fauna are predictable in species content--the ones here are common anywhere." (Comment made at the field site while examining protozoa from meadow soil.)	O.W. Heal, Merlewood, England
Class Mastigophora	
Bodonidae	
1 sp.	
"diflagellate"	
1 sp.	
Anisonemidae	
<i>Entosiphon sulcata</i> (Dujardin) Stein	
Class Rhizopoda	
Order Amoebzoa	
Suborder Amoebina	
<i>Limax</i> sp.	
? <i>Astra</i> sp.	
Suborder Testacea	
<i>Centropyxis aculeata</i> (Ehernberg) Stein	
<i>Cyphoderia ampulla</i> (Ehernberg) Leidy	
<i>Euglypha</i> sp.	
<i>Nebela collaris</i> (Ehernberg) Leidy	
<i>Plagiopyxis</i> sp.	
<i>Trinema enchelys</i> (Ehernberg) Leidy	
<i>T. lineare</i> Penard	
Class Sporozoa	
Subclass Haplosporida	
1 sp. (host: <i>Branchinecta paludosa</i>)	G. Daborn, U. of Alberta
Class Ciliata	
Order Holotrichia	
<i>Hypotrichius</i> sp.	O.W. Heal

the species list, emphasizes the incompleteness of these determinations. I have seen representatives of additional species, but could not make determinations. The Protozoa were tentatively the most significant energy releasers at Truelove. Their low diversity on this list is not a meaningful cross-check on their energetic impact. This is apparently the only Canadian high arctic Protozoa species list. MacLean (pers. comm.) has a list of 20 spp. from Pt. Barrow, complemented by the efforts of Fenchel (1974).

A single specimen of what appears to be a leuconid sponge (Table 17.B), approximately 6 cc, was collected by Heal. The species was apparently rare. Another sponge, approximately 2 cm x 0.75 cm, resembling *Grantia*, was collected on Bathurst Island by P. Lamothe, U. of Alberta. These are the first records of fresh water sponges from the high arctic (but sponges generally are marine organisms, which leaves doubts about the actual collection sites).

The single species of typhloplanid turbellarian was approximately 1 mm long when live and active. Individuals were extracted as amorphous blobs by O'Connor funnels. The species was not abundant, but was widespread in meadows. This is a first arctic record (but is of little value without specific determination). Trematodes, and parasitic turbellarians, were absent.

Tapeworms were found in the intestines of 8 lemmings, *Dicrostonyx groenlandicus* Traill. Uncertainties in the taxonomic literature, and improper preservation, prevented specific determination. Tapeworms were found in numerous arctic char, *Salvelinus alpinus* L., in one walrus, *Odobenus rosmarus*, and in one black guillemot, *Cepphus grylle*. Aquatic and marine animals were beyond the scope of this terrestrial study, so determinations of these specimens were not pursued.

Table 17. B. Lower Metazoa

Taxon	Determined by
Subkingdom Metazoa	
Phylum Porifera	
Class Demospongiae	
Spongillidae	
1 sp.	
Phylum Platyhelminthes	
Class Turbellaria	
Order Neorhabdocoela	J.O. Young, U. of Liverpool
Typhloplanidae	
1 sp.	
Class Cestoda	
3 sp. (hosts: <i>Cephus grylle</i> <i>Odobenus rosmarus</i> <i>Salvelinus alpinus</i> L.)	
Order Cyclophyllidia	R. Hobbs, U. of Alberta
1 sp. (host: <i>Dicrostonyx groenlandicus</i> Traill.)	
Phylum Nematoda	
<i>Cystidicola</i> sp. (host: <i>Salvelinus alpinus</i>)	J.C. Holmes, U. of Alberta
<i>Plectus</i> sp.	D.L.C. Procter, U. of Alberta
Phylum Rotifera	
3 terrestrial sp.	
<i>Filinia</i> sp.	K. Minns, U. of Manitoba
<i>Keratella cochlearis</i> (Gosse)	
<i>K. quadrata</i> (Mueller)	
<i>Polyarthra</i> sp.	
Phylum Annelida	
Class Oligochaeta	
Enchytraeidae	
<i>Bryodrilus parvus</i> Dash(?)	Mahdab Dash, Paul Skydt, U. of Calgary
<i>Cernovitoviella</i> sp.	
<i>Henlea nasuta</i> Eisen	
<i>H. perpusilla</i> Nielsen & Christensen	
<i>H.</i> sp. A	
<i>Marionina</i> sp.	
<i>M.</i> sp.	
Phylum Tardigrada	
Class Eutardigrada	
Pseudechiniscidae	
<i>Pseudechiniscus</i> sp.	D. Nelson, E. Tenn. and R.P. Higgins, Smithsonian Inst.
Macrobiotidae	
<i>Macrobiotus</i> sp.	

Truelove's rotifer fauna was more diverse than this list indicates. Their diversity, and determination, problems parallel those encountered with Protozoa. At least 3 markedly different body shapes were found in terrestrial samples, while K. Minns found specimens of 4 species in lake samples.

The oligochaete list requires further work. The species listed were collected by Paul Skydt in a 2 week period, in 1970; his identifications were confirmed by Mahdab Dash. This time span was too brief to be thorough; but a more complete study should have been made, in view of the energetic importance of enchytraeids. A comparison of this list with enchytraeid lists from other IBP sites (Ryan, 1976) suggests that an additional oligochaete family, and additional enchytraeid species, could occur in the Truelove fauna. Preserved enchytraeids are difficult to determine - live material is required - and 2 prominent taxonomists declined examination of my Truelove specimens. Nurminen (1973) reported the presence of 2 enchytraeid species on Devon Island (not at Truelove), in addition to determining the Char Lake (Cornwallis Island) fauna. His is the only Canadian high arctic work, and is concentrated on lake species. Leeches were never found, despite probable repeated introductions by waterfowl.

There were no terrestrial molluscs at Truelove. Shells and egg cases of marine molluscs were collected on beaches.

Two tardigrade species occur here. My observations indicate that individuals of smaller species, *Pseudechiniscus* sp., were abundant, while those of the larger *Macrobiotus* sp. were rare. This has yet to be confirmed by Dr. D. Nelson, who is presently examining

Truelove specimens.

Arthropod species, particularly insects, received more of my attention than the taxa discussed above. Surface dwelling arthropods, except chironomid flies, are better represented in the list than sub-surface species.

The first 4 crustaceans listed in Table 17.C, plus *Cyclops scutifer* and *Mysis relicta*, are pond inhabitants, while the rest were collected in meadows. *Branchinecta paludosa* and *Lepidurus arcticus* specimens were both conspicuous and large, and were observed to have one generation yr^{-1} . The most abundant copepod species was the harpacticoid *Attheyella nordenskioldii*, which I saw in meadows throughout the lowland; *Eurytemora* sp. was about 0.1 as common. The ostracod species were patchily distributed. Some dwelt in oligotrophic rock pools, as well as in meadows.

The list of Truelove Araneida (Table 17.D) has been published (Leech and Ryan, 1974). A single male *Dictyna borealis* Pickard-Cambridge, and several specimens of *Collinsia thulensis* (Jackson) (Linyphiidae), were also collected and are added to this present list. Leech examined approximately 4000 spiders to find representatives of these 10 species. Nine species are common to Lake Hazen, which supports 13 species altogether (Leech, 1966).

Seven of the 22 mite species listed (Table 17.E) were parasites, with representatives of 5 species occurring on *Bombus polaris*. The *B. polaris* parasite loads were occasionally strikingly heavy, i.e. 4 individuals each carried over 400 relatively large individuals of *Parasitus* sp. *Laelaps alaskensis* was the only terrestrial mammalian arthropod parasite I found. I examined

Table 17. C. Crustacea

Taxon	Determined by
Phylum Arthropoda	
Class Crustacea	
Cohort Branchiopoda	
Order Anostraca	
Branchinectidae	
<i>Branchinecta paludosa</i> (Mueller)	G. Daborn, U. of Alberta
Order Notostraca	
<i>Lepidurus arcticus</i> Pallas	
Order Cladocera	
Daphnidae	
<i>Daphnia pulex</i> Leydig	
Bosminidae	
<i>Bosmina coregoni</i> Baird	K. Minns
Cohort Maxillopoda	
Order Copepoda	
Suborder Calanoida	
Temoridae	
<i>Eurytemora</i> sp. prob. <i>composita</i>	G. Daborn
Suborder Cyclopoida	
<i>Cyclops scutifer</i> Sars	K. Minns
<i>C. vernalis</i> Fischer	
Suborder Harpacticoida	
<i>Attheyella nordenskioldii</i> (Lilljeborg)	H.C. Yeatman, U. of South, Tennessee
Cohort Ostracoda	
Order Podocopa	
Cypridae	
<i>Candona compressa</i> Koch	L.D. Delorme, Calgary
<i>C. willmani</i> Staphlin	
<i>Eucypris crassa</i> (Mueller)	
<i>Prionocypris glacialis</i> (Sars)	
Cohort Malacostraca	
Order Mysidacea	
<i>Mysis relicta</i> Lovén	K. Minns

Table 17. D. Araneida

Taxon	Determined by
Class Arachnida	
Order Araneida	
Dictynidae	R.E. Leech, Ottawa
<i>Diotyna borealis</i> Pickard-Cambridge	
Lycosidae	
<i>Tarentula exasperans</i> Pickard-Cambridge	
Linyphiidae	
<i>Acartauchenius pilifrons</i> (Koch)	
<i>Collinsia spetsbergensis</i> (Thorell)	
<i>C. thulensis</i> (Jackson)	
<i>Diplocephalus barbatus</i> (Koch)	
<i>Erigone psychrophila</i> Thorell	
<i>Hilaira vexatrix</i> (Pickard-Cambridge)	
<i>Minyriolus pamphia</i> Chamberlin	
<i>Typhochraestus latithorax</i> (Strand)	

Table 17. E. Acarina

Taxon	Determined by
Order Acarina	
Suborder Mesostigmata	
Parasitidae	
<i>Parasitus</i> sp. nov. near <i>fucorum</i> (DeGeer)	L. Richards, U. of Kansas
<i>P.</i> sp. nov.	(all L. Richards ident.
Laelapidae	are from <i>Bombus polaris</i>)
<i>Laelaps alaskensis</i> species-	E.E. Lindquist, Ottawa
complex (host: <i>Dicrostonyx</i>	
<i>groenlandicus</i>)	
<i>Pneumolaelaps groenlandica</i> Traegardh	L. Richards
(host: <i>Bombus polaris</i>)	
Haemogamasidae	
<i>Haemogamasus ambulans</i> (Thorell)	E.E. Lindquist
Ascidae	
<i>Arctoseius multidentatus</i> Evans	
<i>A. ornatus</i> Evans	
<i>Cheiroseius groenlandicus</i> (Haarlov)	
Suborder Prostigmata	
Podapolipidae	
<i>Locustacaris buchneri</i> Stammer	L. Richards
Rhagidiidae	
<i>Rhagidia</i> sp. near <i>hamata</i> (Kramer & Neum.)	E.E. Lindquist
Eupodidae	
<i>Cocceupodes curviclava</i> Thor	
Bdellidae	
<i>Bdella muscorum</i> Ewing	
<i>Neomolgus littoralis</i> (L.)	I.M. Smith, Ottawa
Stigmaeidae	
<i>Stigmaeus parvatus</i> Summers	E.E. Lindquist
Lebertiidae	
<i>Lebertia</i> sp.	I.M. Smith
Suborder Astigmata	
Acaridae	
<i>Kuzinia</i> sp. nov. near <i>laevis</i> (Dujardin)	L. Richards
Suborder Cryptostigmata (Oribatei)	
Hermannidae	
<i>Hermannia subglabra</i> Berlese	E.E. Lindquist
Camisiidae	
<i>Camisia horrida</i> (Hermann)	
Eremaeidae	
<i>Eremaeus</i> sp. ?	
Ceratozetidae	
<i>Iugoribates gracilis</i> Sellnick	
<i>Trichoribates lucens</i> (Koch)	
<i>T. polaris</i> Hammer	

approximately 250 specimens of its lemming host, *D. groenlandicus*, and regularly found mites, but I never found heavily infested lemmings. With only 14 species, the soil dwelling Acarina are poorly represented at Truelove. I am certain an acarologist would find representatives of more species in my 363 Tullgren, and Addison's 392 Macfadyen high gradient, extraction samples. Additional sampling, and specialized techniques, would undoubtedly recover specimens of additional species. Pt. Barrow, Alaska, has more than 50 species of soil mites (Hurd and Lindquist, 1958; Bohnsack, 1968).

Soil mite populations m^{-2} , and diversity, were low compared to those of Collembola. The standing crop (c.f. Table 10) ratio of Acarina/Collembola was 0.27 on the intensive study raised beach, and 0.37 on the study meadow. Ecologically immature alpine communities are characterized by a standing crop, and species diversity, dominance of Collembola over predatory and parasitic Acarina (Mani, 1968). This ratio reverses in mature alpine communities. Since the Truelove Lowland rose from the sea about 8700 years ago (Barr, 1971; Bliss, 1977b), it supports an immature ecosystem in the sense meant by Mani. His prediction suggests that the Truelove acarine diversity may not be strikingly under-representative.

Collembola (Table 17.F) were the most abundant arthropods collected at Truelove (however, the model indicates that larval nematoceros Diptera populations are greater). *Hypogastrura* is the dominant genus (Addison, 1975). This group was studied by Addison at Truelove. There is some lack of agreement between the determinations of Richards and Sharp. It is probable that this list names more species than were actually collected (or, more than one or the other

Table 17. F. Collembola

Taxon	Determined by
Class Insecta	
Order Collembola	
Poduridae	
<i>Anurida granaria</i> (Nicolet)	W.R. Richards, Ottawa
<i>Ceratophysella armata?</i> (Nicolet)	
<i>Hypogastrura</i> sp. near <i>trybami</i> (Schoett)	
H. <i>tullbergi</i> (Schaeffer)	
H. sp. 1 near <i>tullbergi</i>	
H. sp. 2 near <i>tullbergi</i>	
H. sp. 3	
<i>Micranurida pygmaea</i> Boerner	J.A. Sharp Addison, U. of
<i>Morulina gigantea</i> (Tullberg)	W.R. Richards / Alberta
<i>Podura aquatica</i> L.	J.A.S. Addison
<i>Willemia anophthalma</i> Boerner	
Onychiuridae	
<i>Onychiurus groenlandicus</i> (Tullb.)	W.R. Richards
O. sp.	
<i>Tullbergia</i> sp. nr. <i>simplex</i> Gisin	J.A.S. Addison
Isotomidae	
<i>Anurophorus?</i> sp.	
<i>Folsomia bisetosa</i> Gisin	
F. <i>duodecimsetosa</i> Hammer	
F. <i>fimetaria</i> (L.)	W.R. Richards
F. <i>quadrioculata</i> (Tullberg)	
F. <i>regularis</i> Hammer	J.A.S. Addison
<i>Isotoma notabilis</i> Schaeffer	
var. <i>pallida</i> Agrell	
I. <i>olivacea</i> Tullberg	W.R. Richards
I. <i>violacea</i> Tullberg	
I. sp. n.	
<i>Isotomurus palustris</i> (Mueller)	
<i>Proisotoma</i> sp. n.	
Entomobryidae	
<i>Entomobrya comparata</i> Folsom	
Sminthuridae	
<i>Megalothorax minimus</i> (Willem)	
<i>Sminthurides malmgreni</i> (Tullberg)	
<i>Sphaeridia</i> sp. prob. <i>pumilis</i> (Kraus.)	

person alone would have determined from the same specimens).

There were no orthopteroid insects in the Truelove fauna.

It was not possible, nor desirable, to collect large numbers of birds and mammals. Therefore, I collected comparatively few lice (Table 17.G) in proportion to the probable total number of Truelove species. I visually examined, and combed, 16 birds, of 9 species, and found 1 or more lice on 8 birds. No lice were obtained from berlese samples of duck nests. From 5 snow buntings, *Plectrophenax nivalis*, I collected 7 lice. The single mammal louse was on a walrus. *Hoplopleura acanthopus* Burmeister is common on *Dicrostonyx groenlandicus* elsewhere in the Arctic (Danks and Byers, 1972; McAlpine, 1965), but none were found on Truelove *D. groenlandicus*. Lice are miniscule in comparison to their hosts, which in turn are rare m⁻². Therefore, I neglected lice in my energy flow calculations.

Thysanoptera were apparently absent from the Lowland. No thrips were collected by any invertebrate researchers, including visiting thrips specialist B.S. Heming. Three species are reported to occur at Lake Hazen (Downes, 1964), but they are not listed in Oliver (1963), who Downes cited as listing them.

There are no Hemiptera (*sensu strictu*) at Truelove. During my 1½ day visit to Pt. Barrow, I collected specimens of both Hemiptera species known to occur there, the leafhopper *Hardya youngi* Beirne and the saldid *Chiloxanthus stellatus* (Curtis). One male of the scale insect, *Chorizococcus altoarcticus* Richards, was found at Truelove. Females have been found only on *Dryas* sp. (Richards, 1964). None were found on Truelove *Dryas* sp., despite intensive studies (for other purposes) of *Dryas integrifolia* by several IBP researchers. I

Table 17. G. Phthiraptera and Homoptera

Taxon	Determined by
Order Phthiraptera	T.M. Clay, London
Suborder Mallophaga	
Philopteridae	
<i>Anatocola rubromaculatus</i> Rudow	
(host: <i>Sommateria mollissima</i>)	
<i>Anatoecus</i> sp.	
(host: <i>Chen nivalis</i>)	
<i>Philopterus</i> sp.	
(host: <i>Plectrophenax nivalis</i>)	
<i>Saemundssonina</i> prob. <i>cephalus</i> (Denny)	
(prob. host: <i>Stercorarius parasiticus</i>)	
Suborder Anoplura	
Echinophthiriidae	
<i>Antarctophthirus trichechi</i> Bohemann	
(host: <i>Odobenus rosmarus</i>)	
Order Heteroptera	
Suborder Homoptera	
Pseudococcidae	
<i>Chorizococcus altoarcticus</i> Rich. W.R. Richards	

sought representatives of the 3 aphid and 2 other scale species known to occur at Lake Hazen (Richards, 1963, 1964; Downes, 1964). Three of their host plant species, *Salix arctica*, *Dryas integrifolia*, and *Taraxacum hyparcticum* (determined at Hazen as *T. arctogenum*) occur at Truelove; *Lesquerella arctica* does not. None were found.

There were no neuropteroid insects at Truelove.

Beetles (Table 17.H) were rare at Truelove. Like Lepidoptera, this well studied group is particularly useful for faunal comparisons. There are at least 58 species known to occur east of 100°W in the Canadian arctic (W.J. Brown, pers. comm.). *Amara alpina* was the commonest Truelove beetle. Approximately 200 adults and larvae were collected beside Truelove Inlet, and along the dolomite cliffs. Five specimens of *Gynpeta* sp. were hand collected, and 3 were found in pitfall traps. The Truelove fauna is so reduced that 4 of these 2.5 mm individuals were spotted from standing height, because their gait differed from that of Collembola. *Hydroporus polaris* inhabits permanent pools and shallow ponds. In 1970, both larvae and adults were abundant in the intensive watershed pond, but were not commonly encountered in later years.

Adult Lepidoptera are attractive to collectors. Consequently, representatives of species in this order have been collected more thoroughly than those in other orders, at Truelove and throughout the Arctic. Absence from a given arctic collection usually means absence, or at least rarity, in the collection area. Individuals of *Colias hecla* Lef. (Nymphalidae), and of the lycaenids *L. feildeni* McLach. and *Plebius aquilo* Bdv., were never seen by camp personnel at Truelove. Individuals of *Colias hecla* were reported to be common at

Table 17. H. Lower Endopterygota

Taxon	Determined by
Order Coleoptera	
Carabidae	
<i>Amara alpina</i> Paykull	G.E. Ball, U. of Alberta
Dytiscidae	
<i>Hydroporus polaris</i> Fall	J.L. Carr, Calgary
Staphylinidae	
<i>Gynpeta</i> sp.	J.M. Campbell, Ottawa
Order Trichoptera	
Limnephilidae	
<i>Apatania zonella</i> Zett.	G.B. Wiggins, Ontario
Order Lepidoptera	
Nymphalidae	
<i>Boloria chariclea</i> Schneid.	D. Pforr, U. of Alberta
<i>B. polaris</i> Bdv.	
Noctuidae	
<i>Anarta richardsoni</i> Curtis	E.W. Rockburne, Ottawa
<i>Lasiestra</i> sp.	
<i>Sympistris labradoris</i> Staud.	
Lymantriidae	J.A. Downes, Ottawa
<i>Gynaephora</i> (=Byrdia) <i>groenlandica</i> (Homeyer)	
<i>G. (=B.) rossii</i> (Curtis)	D. Ferguson, USDA
Geometridae	
<i>Dasyuris punctipes</i> Curtis	K. Bolte, Ottawa
<i>Psychophora sabini</i> Kirby	
Pyrallidae	
<i>Udea torvalis</i> Moesch.	G. Lewis, Ottawa
Pterophoridae	
<i>Stenoptilia mengeli</i> Fern.	
Olethreutidae	
<i>Aphania frigidana</i> Pack	
<i>Olethreutes inquietana</i> Wlk.	J.A. Downes
<i>O. mengelana</i> Fern.	

Wolf Valley, on Axel Heiberg Island, by visiting Devon Islanders (Pattie, pers. comm.). These species were absent from the Truelove fauna. The distribution patterns of arctic Lepidoptera species are distinct enough to allow the origins of this fauna to be discussed (Downes, 1966). This reference also lists host plants of abundant species.

Several hundred *B. chariclea* and *B. polaris* specimens were observed flying every year. Truelove individuals are darker than specimens collected from more southerly locations, and have been used to demonstrate progressive melanization with increasing latitude (K. Phillips, pers. comm.). *Boloria polaris* individuals have been observed flying at Truelove while most of the ground was still snow covered. Individuals of *Anarta richardsoni* were the commonest noctuids. I could have taken more than 100 specimens each year, except perhaps in 1972. In total, less than 10 specimens of *Lasiestra* sp. and *Sympistris labradoris* were collected. Individuals of both *Gynaephora* sp. were commonly found as larvae, but I saw only 4 flying adults. Individuals of the geometrid *Psychophora sabini* were most abundant on the granitic north coast. Specimens of *Dasyuris punctipes*, and *Udea torvalis*, were collected twice. Four individuals of the pterophorid, *Stenoptila mengeli*, were collected in the Truelove River Valley; none were found on the Lowland. I collected one specimen of *Aphania frigidana*. Representatives of the 2 *Olethreutes* species were the most abundant Lepidoptera on the Lowland. Individuals of *O. inquietana*, the smaller species, were commonly spotted making 0.5 - 1 m flights, then pausing on the ground. *O. mengelana* individuals made longer flights and were most frequently captured in the air.

They require 2 or more years to mature (MacKay and Downes, 1969).

Diptera is the most diverse insect order at Truelove, and elsewhere throughout the Arctic. Flies possess numerous preadaptations to arctic conditions (Ryan, 1976). Dispersal ability is one feature. Each year muscids, anthomyiids, and calliphorids were observed flying when the Lowland was completely snow covered, as early as May when air temperatures were as low as -15 C. Flight activity extended beyond my departures in late August, when cold storms were common.

Trichocerids (Table 17.I) were abundant each year. Specimens of *Trichocera columbiana* were commonly found in and around lemming burrows. The 2 Truelove species are distributed exclusively in arctic areas (Dahl, 1967). Tipulids were the largest Lowland Diptera. I found larvae and adults in the stomachs of several Truelove insectivorous bird species, so they are favored prey. All Truelove tipulids are winged and capable of flight, as were all the Lowland Diptera I collected. Several Pt. Barrow Diptera, including the tipulid *Pedicia hanna*, are wingless or brachypterous and incapable of flight (MacLean, 1973).

The mosquito (Culicidae) season on the Lowland lasted approximately 2 weeks (late July through early August). Reports from the intensive study sites indicated only 3-4 days of "intensive" mosquito activity per year (1971-73), with a normal maximum of 20 harassing a person at one time. They flew sluggishly, and frequently flew away, without feeding, after landing on people. Adults were most abundant in 1970. This relates to a June 26 Chinook, which melted 22 cm of snow, causing widespread flooding and creating extensive pools, which became larval habitats. In 1971, Colin Hergert

Table 17. I. Nematocerosus Diptera

Taxon	Determined by
Order Diptera	
Trichoceridae	
<i>Trichocera columbiana</i> Alex.	H.J. Teskey, Ottawa
<i>T. borealis</i> Lackschewitz	
Tipulidae	
<i>Dactylolabis rhionoptylodes</i> (Alex.)	
<i>Nephrotoma lundbecki</i> (Nielsen)	
<i>Tipula arctica</i> Curtis	
<i>T. thulensis</i> Alex.	
Culicidae	
<i>Aedes impiger</i> (Walker)	L. Forster, Ottawa
<i>A. nigripes</i> (Zetterstedt)	
Ceratopogonidae	
<i>Ceratopogon (Isohelea)</i> sp.	
Chironomidae	D.R. Oliver, Ottawa
<i>Chaetocladius holmgreni</i> (Jacobsen)	
<i>Corynoneura</i> sp.	
<i>Cricotopus tibialis</i> (Meigen)	
<i>C.</i> sp.	
<i>Diamesa arctica</i> (Boheman)	
<i>D. germinata</i> Kieffer	
<i>D. simplex</i> Kieffer	
<i>Diplocladius bilobatus</i> Brundin	
<i>Heterotrissocladius subpilosus</i> (Kieffer)	
<i>Limnophyes</i> sp.	
<i>Metriocnemus</i> sp.	
<i>Orthocladius (Eudaetylocladius)</i>	
<i>mixtus</i> (Holmgren)	
<i>O.</i> (E.) sp.	
<i>Paracladius alpicola</i> (Zett.)	
<i>Parakiefferiella</i> sp.	
<i>Paraphaenocladius despectus</i> (Kieffer)	
<i>Procladius culiciformis</i> (Linne)	
<i>Psectrocladius</i> sp. (Edw.)	
<i>Smittia velutina</i> (Lundbeck)	
<i>Thienemanniella</i> sp.	
<i>Trissocladius</i> sp.	
Mycetophilidae	
<i>Boletina</i> sp. 21	J.R. Vockeroth, Ottawa
<i>Bolitophila</i> n. sp.	
<i>Erechia frigida</i> (Boh.)	
Sciaridae	
<i>Bradysia</i> spp. (about 4-5 spp.)	B.V. Peterson, Ottawa
Cecidomyiidae	
<i>Campylomyza</i> sp.	J.F. McAlpine, Ottawa

sampled all water bodies, on half the Lowland, searching for mosquitos. He found no larvae or pupae despite concerted effort, even in ponds which had abundant larvae in 1970. I concluded from this that mosquitos were actually uncommon on the Lowland, and that they were an energetically insignificant group there. They appeared important because they sought human hosts, and were an annoyance. The only other biting fly, *Ceratopogon* sp., was rare. There were no reported human bites by *Ceratopogon* sp. adults - this species feeds on chironomid flies (Downes, pers. comm.).

Chironomids are the most diverse taxon at Lake Hazen (Oliver, 1963), which in part reflects Oliver's interests as a chironomid systematist. They are diverse, and were the most abundant pterygote insects, at Truelove. The list contains 13 species collected by Oliver on a Truelove visit in late August, 1960, as well as results of my own collections. Much material is still awaiting determination. I was not keen to collect and mount these dismal insects, so my list under-represents their actual diversity. Sciarids are the next most abundant group of nematocerous Diptera, but all belong to an unresolved species complex in the genus *Bradysia*. Larvae of at least one Mycetophilid species (apparently *Boletina* sp. 21) inhabit mushrooms, while adults of *Erechia frigida* were collected in emergence traps, with no mushrooms seen inside. Specimens of the cecidomyiid *Campylomyza* sp. were rare, and adults were collected only in the hydric meadow 2 km northwest of camp. Red larvae collected on female *Salix arctica* catkins in 1970 may be of this, or of another, cecidomyiid species - these larvae were lost, preventing confirmed identification.

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Short horned flies (Brachycera) (Table 17.J) are represented by 2 families, Empididae and Dolichopodidae, at Truelove. The empidids are conspicuous predators, and were frequently collected. Feeding and mating behavior of individuals of arctic *Rhamphomyia* species have been described (Downes, 1970). Specimens of *Dolichopus humilis* were infrequently collected, most being found in the Truelove Inlet area.

Cyclorhaphous flies are dominated in abundance and species diversity by the Muscoidea. Other families are poorly represented. Larvae and adults of *Melanostoma* sp., the only syrphid, were all collected (infrequently) on the south-facing slope of Truelove Inlet. Larvae of *Arctopiophila arctica* and *P. fulviceps* are bone cleaning scavengers. Muskox cranial cavities are frequently crammed with pupal cases of these flies, and larvae and adults were collected from cartilage between bones of a bull dead about 4 years. Individuals of the 2 heleomyzid fly species were occasionally collected every year; they were uncommon but not rare.

In 1970, scatophagids were more frequently encountered than in 1971-72. This change may be due to a shortage of dung, the larval habitat, which would reflect changes in muskox grazing patterns. Summer dung falls in larger piles than the winter "marbles", is fresher, and is more favorable for breeding. It is possible that our research team's presence, in summer, drove muskox to adjacent lowlands; or, alternatively, that dung deposition reflected a natural yearly variation in lowland usage by muskox.

I was unable to distinguish muscid species in the field. Approximately 550 specimens were determined to species. Emergence

Table 17. J. Higher Diptera

Taxon	Determined by
Empididae	
<i>Clinocera</i> n. sp.	H.J. Teskey
<i>Rhamphomyia hoeli</i> Frey	9
<i>R. nigrita</i> Zett.	
Dolichopodidae	
<i>Dolichopus humilis</i> Van Duzee	
Syrphidae	
<i>Melanostoma</i> n. sp.	J.R. Vockeroth
Piophilidae	
<i>Arctopiophila arctica</i> Holmgren	J.F. McAlpine
<i>Piophila fulviceps</i> Holmgren	
Heleomyzidae	
<i>Aeciothea specus</i> (Aldrich)	B.V. Peterson
<i>Neoleria prominens</i> (Becker)	
Scatophagidae	
<i>Allomyella unguiculata</i> Mall.	J.R. Vockeroth
<i>Scatophaga apicalis</i> Curtis	
<i>S. nigripalpis</i> Becker	
Muscidae	
<i>Spilogona almquisti</i> (Holmgren)	D.M. Wood, Ottawa
<i>S. deflorata</i> (Holmgren)	
<i>S. dorsata</i> (Zett.)	
<i>S. latilamina</i> (Collin)	
<i>S. melanosoma</i> (Huckett)	
<i>S. obsoleta</i> (Mall.)	
<i>S. tundrae</i> (Schnabl.)	
Anthomyidae	
<i>Fucellia ariciiformis</i> Holmgren	J.F. McAlpine
<i>F. pictipennis</i> Becker	
<i>Hylemya (Delia) fasciventris</i> Ringdahl	
Calliphoridae	
<i>Boreellus atriceps</i> (Zett.)	B. Cooper, Ottawa
<i>Protocalliphora sapphira</i> (Hall)	P. Graham, London, England
(host: <i>Plectrophenax nivalis</i>)	
<i>Protophormia terraenovae</i> (R.D.)	B. Cooper
Tachinidae	
<i>Spoggosia gelida</i> (Coq.) (hosts:	D.M. Wood
<i>Gynaephora groenlandica</i> & <i>G. rossii</i>)	

trap records show that several were soil dwellers, probably inhabiting decaying vegetation. Specimens of the anthomyiid *Fucellia ariciiformis* bred in seaweed along the coast, but individuals of both *Fucellia* species were collected all over the lowland. Specimens of *Hylemya fasciventris* were the least common of the anthomyiids.

Adults of the calliphorids *Boreelus atriceps* and *Protophormia terraenovae* were both collected from a muskox carcass, with *P. terraenovae* being decisively more abundant. Only *B. atriceps* specimens were collected at Ellef Ringnes and Bathurst, even in muskox carcasses (McAlpine, 1965; Danks and Byers, 1972). Some individuals of both species completed development in one Truelove summer, 1971, on this muskox, which had died earlier in the spring. Most were still larvae by summer's end. Heat generated during decomposition - the carcass was much warmer than ambient - accelerated larval growth, compared to that of larvae in a 400 g piece of muscle I removed from the carcass. During the succeeding winter, foxes consumed the remains of the carcass, eating maggots as well as rotten flesh. In effect, the blow flies and foxes competed to decompose this corpse. Random Lowland collections gave approximately equal numbers of both species. *P. terraenovae* adults were collected at a Truelove gull rookery, and from a lemming carcass at Ellef Ringnes (McAlpine, 1964). One *Protocalliphora sapphira* larva was collected from the back of a young snow bunting.

Specimens of the only Lowland tachinid, *Spoggosia gelida*, were reared from larvae of both *Gynaephora groenlandica* and *G. rossii*.

Tenthredinids (Table 17.K) are important herbivores on willow in the southern Jamal, USSR tundra site (Bogatschova, 1971). At

Table 17. K. Hymenoptera

Taxon	Determined by
Order Hymenoptera	
Suborder Symphyta	
Tenthredinidae	
<i>Amauronematus</i> nr. <i>abnormus</i> <i>A.</i> nr. <i>alpacola</i> <i>A.</i> nr. <i>anthracinus</i> <i>A.</i> nr. <i>atratus</i> <i>A.</i> nr. <i>coracinus</i> <i>A.</i> nr. <i>histrion</i> <i>A.</i> nr. <i>leucolaenus</i> <i>A.</i> nr. <i>moluckliei</i> <i>A.</i> nr. <i>opacipleuris</i>	W.R. Wong, Edmonton
<i>Pristiphora</i> n. sp.	
Suborder Apocrita	
Braconidae	
<i>Apanteles</i> n. sp. 130 <i>A.</i> n. sp. 133 (host: <i>Anarta richardsoni</i>)	W.R.M. Mason, Ottawa
<i>Microplitis</i> n. sp.	
<i>Oresbius tibialis</i> Tow.	
<i>O.</i> <i>trifasciatus</i> Ashm.	
<i>O.</i> n. sp.	
<i>Rogas</i> n. sp. (hosts: <i>Gynaephora</i> <i>groenlandica</i> & <i>G. rossii</i>)	
Ichneumonidae	
<i>Atractodes</i> spp. (several spp.)	
<i>Bathythrix</i> n. sp.	
<i>Camptocryptus</i> spp. (2 spp.)	
<i>Cryptus leechi</i> Mason	
<i>Diadegma</i> sp.	
<i>Glypta</i> sp.	
<i>Hyposoter</i> sp.	
<i>Ichneumon lariae</i> Curtis	
<i>I.</i> n. sp.	
<i>Mesoleius</i> n. sp.	
<i>Orthocentrus</i> sp.	
<i>Plectiscus</i> n. sp.	
<i>Stenomacrus femoralis</i> Holmgren	
<i>S.</i> sp. U	
<i>S.</i> sp.	
<i>Trathala</i> n. sp.	
Encyrtidae	
<i>Copidosoma</i> sp.	C.M. Yoshimoto, Ottawa
Pteromalidae	
<i>Seladerma</i> n. sp.	
Apidae	
<i>Bombus (Alpinobombus) polaris</i> Curtis	K.W. Richards, U of Kansas

Truelove, larvae were observed on willow, but they were never notably abundant. The family requires extensive taxonomic revision, especially the genus *Amauronematus* (Wong, pers. comm.). Dr. Wong determined specimens to be near to the *Amauronematus* species listed, but not necessarily to be of these species. This taxonomic chaos prevents meaningful comparisons of tenthredinid faunas from different tundra sites.

Most Truelove Apocrita were parasites, except *Bombus polaris*. In most cases, hosts were not known because the wasps were collected in pitfall traps or sweep samples. Specimens of the braconid *Apanteles* n. sp. 133 were reared from *Anarta richardsoni* larvae (host determined by deduction: 2 *Apanteles* cocoon clusters were found with noctuid larva hosts; 5 additional cocoon clusters were found; specimens of *A. richardsoni* were common, while those of the other noctuid species were rare). No Truelove *Apanteles* individuals were reared from *Gynaephora* larvae; Bruggemann reared *Apanteles* adults from *Gynaephora* at Alert, Ellesmere Island (Mason, pers. comm.). *Rogas* sp. adults were reared from larvae of both *Gynaephora* sp. *Bombus polaris*, a ground-nesting bumblebee (Richards, 1973), is often parasitized by *B. hyperboreus* (Schoenh) (Milliron and Oliver, 1966). Individuals of this parasitic species were not collected at Truelove. *B. polaris* adults were seen regularly at Truelove, but were not abundant, and only 2 nests were found.

7.4 Discussion

Table 17.A-K lists the invertebrate species actually found on the Truelove Lowland. Voucher specimens are deposited in the

Strickland Museum, Department of Entomology, University of Alberta, the Canadian National Collection, and occasionally have been kept by the determining specialists. Absence of a particular species from the list means it was not collected, or not identified among the collected specimens. It does not necessarily mean a species was absent from the Lowland, although, for most arthropods, it implies that the species was uncommon. Introduction of species will add temporarily, and permanently, to the fauna. The isolation of Truelove Lowland by 700 Km of severe environmental barriers to the south, including the surrounding glacier, and Arctic Ocean, minimizes this effect. Population numbers fluctuate over time (Andrewartha and Birch, 1954), so some species not collected in this investigation should be common, and presently common species rare, in a future follow-up study.

Species truly not a part of the Lowland fauna may be absent because: 1) they can not live there, or 2) they never got there. Certainly, many species have been introduced during the 8700 year existence of the Lowland. Migrating waterfowl probably carried in leeches, rotifers, crustaceans, and other invertebrates, as well as aquatic plants. Some of these species became established. Leeches, likely phoretic animals, have not established at Truelove, so it is probable that they can not live there. Damselflies might be able to establish themselves and reproduce in the high arctic, but have not arrived there (Corbet, per. comm. speculation).

Comparison with other arctic faunas is instructive. The Lake Hazen (82°N 71°W, Ellesmere Island) fauna was investigated by a

professional insect survey team for 1 season, followed by several seasons of student study. The published fauna (mainly, Oliver, 1963) is incomplete (Downes, pers. comm.). Despite its more northerly latitude, Lake Hazen has a mean 397 C degree days above 0 C (1967-68 seasons, 1.5 m Stevenson screen, Corbet and Danks (1974)), while the Truelove Lowland season was 304 C degree days (meadow site, Appendix 8.D.II). Lake Hazen is inland, so higher temperatures than those recorded at coastal Truelove are understandable. Also, summer "night" temperatures are ameliorated at higher latitudes (Corbet, 1969). Both factors make summer at Lake Hazen 1.4-fold warmer/longer than at Truelove. Lake Hazen supports 115 species of vascular plants (Saville, 1972), while Truelove has 96 (Barrett and Teeri, 1973; Bliss, 1977a). Therefore, the Lake Hazen fauna should be more diverse than Truelove's.

Lake Hazen supports approximately 222 species of arthropods (213 listed by Oliver, 1963). Truelove has 198 known arthropod species. The difference is largely in the number of chironomids. Hazen has 6 species of Homoptera, while one homopteran species is known from Truelove. Numbers of species present in comparable - well studied - taxa at Lake Hazen/Truelove are: Araneida 13/10, Coleoptera 3/3, Lepidoptera 17/14, Diptera Culicidae, Empididae, Dolichopodidae, Syrphidae, Calliphoridae, Tachinidae 16/11, Hymenoptera Apocrita (except *Atractodes* sp.) 35/26. Thus, arthropod species diversity is greater at Lake Hazen.

Pt. Barrow Alaska, at 72°N 156°W, has a 321 degree day season. (Note: Stevenson screen temperatures are only approximately relevant to biological processes. I use them here only for comparative

purposes.) It supports a flora of 95 vascular plant species. The Barrow fauna was investigated at separate times by 2 professionals, and assistants. Temperatures, and the flora, at Barrow are quite similar to those of Truelove. However, Pt. Barrow is a low lying extension of a continental land mass. It is near enough to the Pleistocene era Bering land bridge to show faunal influence from Soviet Asia (Ryan, 1976). Truelove Lowland is on an island (see MacArthur and Wilson (1967) for a discussion of species diversity on islands), and is not near any sites of notable faunal interchange.

Barrow supports approximately 345 known arthropod species, and the total fauna is estimated to be 400-450 species (Bohnsack, 1968). The fauna is distinctly more diverse than Truelove's. Some of the numerical difference reflects the interests of investigators (especially the more than 50 soil mite species, determined by Lindquist, versus 14 at Truelove). Other differences, such as Barrow's 14 Coleoptera and 5 Lepidoptera species, versus Truelove's 3 Coleoptera and 14 Lepidoptera species, are due to differences between the sites. Barrow experiences a longer open ocean period, so it is foggier and damper, and less favorable to Lepidoptera than Truelove. The greater beetle fauna probably relates to its continental position, which permitted easier invasion by beetles, as well as by the rest of the fauna. In a 1½ day visit to Barrow I collected insect species which do not occur at Truelove. My impression was that the vegetation there was similar, or slightly more lush, but that the arthropod fauna was both more diverse, and different. Individual Collembola were larger than any I saw at Truelove (except *Morulina gigantea*). Population numbers of enchytraeids, mites, and Collembola

are generally greater at Barrow than at Truelove (MacLean, 1976). Thus, there are real differences between Barrow and Truelove, despite numerous similarities. These differences are due to Barrow's continental status, and its more southerly, western arctic position.

Ellef Ringnes, at 79°N 98°W, with an estimated 70 species of vascular plants, could be expected to have more arthropods than the 48 species (excluding chironomids) reported. Both sites were investigated for only a partial season, without extraction apparatus, by one, and 2, researchers respectively. The authors stressed that their faunal lists were not complete. Specimens of only one lepidopteran, *P. sabini*, and no Coleoptera, were collected at both sites. Although these lists are incomplete, they show clearly that the faunas of the Bathurst and Ellef Ringnes sites are depauperate compared to that of Truelove.

Compared to other IBP tundra sites (Ryan, 1976), the Truelove Lowland fauna is the least diverse, and is probably similar to the USSR Wrangel Island subsite. Barrow comes next, then Tareya (Taimyr, USSR). The Scandinavian sites are next, and are similar. Of these Hardangervidda (Norway) appears to be the least, Kevo (Finland) intermediate, and Stordalen Mire (Sweden) the most, diverse. The U.K. sites are comparatively the most diverse in the tundra biome, Glenamoy (Ireland) being less, and Moor House (England) being more, diverse. These last sites are desolate mires, not actually tundra sites.

Chapter 8

CONCLUSION

I shall use this chapter to comment on, and criticise, some conclusions from the thesis. This should give a perspective on its contents, and on possible directions of future energetics, and arctic, research.

The many-faceted nature of this thesis makes it difficult to co-ordinate the information presented to a single conclusion. The chapters are written as self-sustaining units, each containing its own conclusions. The whole of the thesis is support and documentation for the energy flow conclusions of Table 15. Figure 9 illustrates these conclusions, relates them to the ecosystem, and defines energy flow.

I refer to my energy flow conclusions as hypotheses, while other publications present such data without this disclaimer. Energy flow through invertebrates is inherently subject to numerous possible measurement errors, including those of population size and structure, growth and death rates, respiration rates, consumption rates, and so on. As an illustration of this error range, consider respiration. Measuring the respiration rates of a few individuals of a species, for short time periods, while they are exposed to highly unnatural conditions (altered humidity, removed from food, unnatural substrate), provides a rather tenuous base from which to extrapolate the accumulated lifetime respiration of even one individual of that species. The temperature regime experienced by this individual, in nature, will differ drastically from laboratory respirometer conditions. One could reasonably allow the possibility of 2 decimal

place accuracy when the lifespan respiration of one individual is calculated, but the second figure would be doubttable even following detailed study. Yet, respiration rate is the most accurately measureable of all energy flow parameters. Because the inherent error range is so large, I suggest that the results of all invertebrate energetics studies, particularly broadly based ones, are more accurately described as hypotheses than as discretely quantified data.

Energy flow was determined with a model, which is composed of challengeable statements about attributes of invertebrate populations. The conclusions by this time are based on so little hard data that they have been criticised as being useless. This criticism indicates a fundamental lack of understanding of the model. I shall indicate why this is so by reconsidering the model here.

All invertebrate taxa (except Protozoa and Nematoda) were analysed with the model. This imposes a consistency to ranking the energy flowing through all the invertebrate taxa. The ranking itself is a significant result.

The input parameters for each model taxon are subject to reinterpretation, and may appear to be a major possible source for error. Energy flow in the model is overwhelmingly determined by standing crops, respiration rates, and temperatures. The size ranges of individuals, the number of eggs deposited, and the caloric values of tissue have minor impacts on the calculated energy flow, as was shown in Table 7. The Respiration/Production ratios, and biological factors such as cryptobiosis, affect the results more. A radical restructuring of the input parameters used for the

model could halve, or double, the energy flows I report. However, no radical restructuring appears to be necessary. Where mistaken inputs exist, they are likely to occur throughout all the model taxa. Thus, the same ranking of taxa by energy flow magnitudes will be preserved.

My strongest reservations about the model inputs lie with the $R/P = c$ ratios. These "c" ratios determine the maturation times of animals, with higher "c" values causing longer maturation times. I used minimal values for "c", which were frequently 20-30% less than values calculated from published feeding/growth studies. I am now inclined to accept higher "c" values than were used in the text, which would result in longer predicted lifespans. The lifespans presently predicted exceed the privately held expectations of several researchers at the Biosystematics Research Institute in Ottawa (Downes, pers. comm.), and with revised "c" ratios they would be even longer. The model has generated testable hypotheses on the maturation times required by arctic insects, and intimates that these predicted times may be underestimates.

Three basic assumptions of the model address problems of measuring respiration for the entire weight-span of organisms, and of calculating tissue production at the time of death of these animals. This represents a refinement over existing energetics technology, as no other community based study has dealt effectively with these problems.

In the thesis introduction I outlined reasons why the Truelove site was ideal for a study of invertebrate energetics. The reduced diversity did not allow me to be distracted by

comparatively spectacular but otherwise (energetically) unimportant insects, and thus forced my attention to the activities of soil invertebrates. Most invertebrate energy flow was found to occur in the soil. I found evidence that protozoa play the leading energetic role for the meadow invertebrates. This group is almost always excluded from consideration in warmer climate studies, because they are so technically difficult to work with. The (comparative) simplicity of conditions at the Truelove site allowed me to consider aspects of invertebrate population biologies that I could not have done elsewhere. Some striking conclusions resulted. For example, the oribatid mites were found to have 30-60 year maximum lifespans. This comes from the model analysis, and would have been difficult to realize from a purely empirical approach. The model produced answers for the questions asked, and generated numerous testable hypotheses in its wake. This study was part of a well co-ordinated, integrated research effort, and its conclusions do not conflict with the results from these independent studies. In fact, they fit together well.

All the broadly based invertebrate studies cited in my literature review contain faults. I believe that this study is more accurate than any of these general studies, and that its component parts are of a comparable accuracy to the best of the cited studies on ecosystem components. At the same time, I will be pleased if the first figures of my energy flow conclusions are correct. I readily admit that they may not be. This has been interpreted to mean that this undertaking was a useless exercise, but that criticism falls equally on all energy flow studies, and

on the field of ecology, as it does on this thesis.

The quantitative data in chapter 5 can be used in many ways besides the determination of energy flow. Some can be used to diagrammatically represent the structure of the Truelove ecosystem. The structure of the meadow site, in numbers of species and organisms, and standing crop biomass, is shown in Figure 10 (partially reprinted from Bliss (1977b)). The information on which the invertebrate data of Figure 10 is based is contained within this thesis, although not in this same form. MacLean (1976) used this Truelove data in a comparison of the IBP tundra sites.

Sweep net sampling yielded information about the distribution of winged insects on the Lowland. It showed concentrations of chironomid flies around lakes, which led to the hypothesis that their bodies could return significant amounts of nitrogen from lakes to the land. Emergence trap results, and revised nitrogen synthesis rates, showed that the quantity deposited was about 4% of that synthesized yearly, not a significant addition. The sweep net samples gave a rough comparison of winged insect populations over the 1970-72 period. Truelove sweep net results can be compared to results from other areas. It is not included here, but I have compared Janzen and Pond's (1975) sweep net comparisons from tropic and temperate sites, to Truelove site results. Comparisons of this type can also be made with the pitfall trap, and emergence trap, data. The emergence traps provided the most precise production data in this thesis.

Gynaephora groenlandica and *G. rossii* are cold-adapted insect species. The details of the chapter 3 study of these insects help to determine why, and how, a few selected species can survive in an

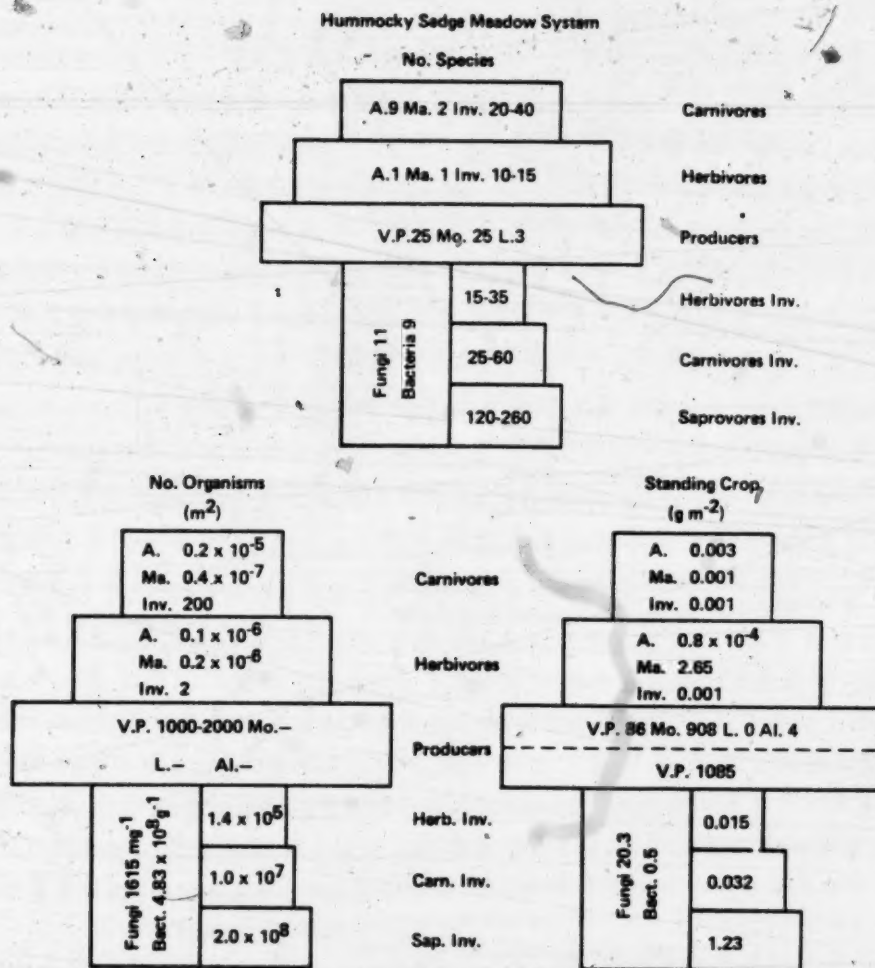


Fig. 10. Diagrammatic representations of the structure of the meadow study site

environment unsuitable to so many other species. The hypothesis of opportunism by arctic insects (Downes 1964, 1965) is challengeable with data contained in this thesis, particularly in this chapter. Inconsistencies found in larval *Gynaephora* respiration rates, and accompanying inactivity, the cessation of feeding, and the inception of pupation, indicate a state of diapause occurred. Such regulated timing conflicts with the concept of opportunism. One may ask why diapause, an adaptation to winter, should be thought to be absent in these coldest environments. Part of the answer may be that diapause does occur in the Arctic, but that it is hard to detect, and separate, from cold-stupor under constantly cold conditions.

The study is a separate energy budget, calculated by a long-hand method rather than by the short-hand of the model. The results of the 2 methods agree well: 3.3 cal for *Gynaephora*, and 32 cal for all Lepidoptera, assimilated m^{-2} at the raised beach site. The method of relating standing crop measurements to life table data is illustrated more clearly here than later in the model. This procedure is new. The discussion on the role of invertebrate herbivores is based on quantitative energetics data, and qualitative logic. As a generalization about the structure of ecosystems, it contributes a new insight to a view of the world as an ecosystem.

The terminology and methodology of invertebrate energetics are as inconsistent as is the species concept of taxonomists. Some definitions pander to the methodologies of primary production measurements, promising consistency but dubious objectivity to the results of whole ecosystem studies. I distilled my own definitions, allied to Odum's (1971) primary production orientation, from this

quagmire. The distinctions are largely polemic. Errors inherent to the measurement of production will probably cause more divergence in the results from isolated studies than differences caused by using most definitions of production.

The list of invertebrates inhabiting the Truelove Lowland can have several applications, besides its basic purpose of documenting the species included in the energy flow assessment. These species form a source list for subjects of studies on arctic adaptations. The diversity of the listed species, and widespread distributions of any of these species, may be used to prove that chance is a significant factor in the composition of polar faunas. The composition of the Truelove fauna could be re-examined after several decades, to test hypotheses on polar migration rates and faunal stabilities. Such a study should encompass selected groups, as Lepidoptera, Coleoptera, and certain of the Diptera. Assuming that transport facilities will continue to improve, this project ought to include the Lake Hazen site, and perhaps Pt. Barrow, Alaska. This, and other complete studies on polar faunas, may be used for comparisons with faunas elsewhere.

The Arctic is bleak, desolate, and expansive. Our civilization has thrust itself into this region in a search for energy, and for benefits to mankind. On the crest of this wave into the Arctic, we have established a laboratory. It provides a view of an extreme zone of the earth. Man obviously has radically altered his environment in the inhabited areas of the world. This laboratory may offer future generations an opportunity to measure man's impact on one last, major, virtually uninhabited portion of the earth.

LITERATURE CITED

- Addison, J.A. Sharp. 1975. Ecology of Collembola at a high arctic site, Devon Island, N.W.T. PhD thesis. Biology Dept., Univ. Calgary. 212 p.
- Addison, J.A. Sharp. 1977. Population dynamics and biology of Collembola on the Truelove Lowland. (in press). In: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Addison, J.A. Sharp. (pers. comm.) Dept. of Zoology, Univ. Alberta, Edmonton, Alberta.
- Allen, K.R. 1971. Relation between production and biomass. J. Fish. Res. Board Can. 28: 1573-1581.
- Andrewartha, H.G. and L.C. Birch. 1954. The Distribution and Abundance of Animals. Chapman, London. 782 p.
- Aurivillius, C. 1883. Insektlifvet i arktiska laender. Studier och forskningar foeranledda af mina i hoega norden. p. 403-459. A.E. Nordenskioeld (ed.). F. & B. Beijers Foerlag, Stockholm. Transl. by S. Nimmo. 1970. In: Insect Life in Arctic Lands. P.G. Kevan (ed.). Boreal Institute, Alberta. 69 p.
- Babb, T.A. 1974 (unpubl. report). Hypothetical Devon Island meadow nitrogen flows. 5 p. IBP project meeting, Kananaskis Research Station, Alberta.
- Bailey, C.G. 1976. A quantitative study of consumption and utilization of various diets in the bertha armyworm, *Mamestra configurata* (Lepidoptera: Noctuidae). Can. Entomol. 108: 1319-1326.
- Bailey, C.G. and P.W. Riegert. 1973. Energy dynamics of *Encoptolophus sordidus costalis* (Scudder) (Orthoptera: Acrididae) in a grassland ecosystem. Can. J. Zool. 51: 91-100.
- Barnes, R.D. 1968. Invertebrate Zoology. W.B. Saunders Co., Toronto. 743 p.
- Barr, W. 1971. Post-glacial isostatic movement in northeastern Devon Island: a reappraisal. Arctic 24: 249-268.
- Barrett, P.E. and J.A. Teeri. 1973. Vascular plants of the Truelove Inlet region, Devon Island. Arctic 26: 58-67.

- Barsdate, R.J., R.T. Prentki, T. Fenchel. 1974. Phosphorus cycle of model ecosystems: significance for decomposer food chains and effect of bacterial grazers. *Oikos* 25: 239-251.
- Behan, V. 1973 (unpubl. report). Report on Irish IBP invertebrate projects. IBP working group meeting. August, 1973. Univ. Alaska, Fairbanks.
- Beirne, B.P. 1955. Collecting, Preparing and Preserving Insects. Publ. 932. Can. Dept. Agri. 133 p.
- Bierle, D.A. 1972. Production and energetics of chironomid larvae in ponds of the arctic coastal tundra. p. 182-186. In: S. Bowen (ed.). Proc. Tundra Biome Symp. Univ. Washington, Seattle. 211 p.
- Birch, L.C. and P.D. Clark. 1953. Forest soil as an ecological community, with special reference to the fauna. *Q. Rev. Biol.* 28: 13-36.
- Bjarnov, N. 1972. Carbohydrases in *Chironomus*, *Gammarus*, and some Trichoptera larvae. *Oikos* 23: 261-263.
- Blackith, R.E. 1974. The ecology of Collembola in Irish blanket bogs. *Proc. R. Ir. Acad. Sect. B* 74: 203-226.
- Bliss, L.C. 1975. Devon Island, Canada. p. 17-60. In: T. Rosswall and O.W. Heal (eds.). Structure and Function of Tundra Ecosystems. *Ecol. Bull.* 20. Swedish Nat. Sci. Res. Council, Stockholm. 450 p.
- Bliss, L.C. 1977a. Vascular Plant species list. 3 p. (In press). Appendix in: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Bliss, L.C. (ed.). 1977b. (in press). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Block, W. 1965. The life histories of *Platynothrus peltifer* (Koch 1839) and *Damaeus clavipes* (Hermann 1804) (Acarina: Cryptostigmata) in soils of pennine moorland. *Acarologia* VII; 735-743.
- Bogatschova, I.A. 1972. Leaf-eating insects on willows in tundra biocenoses of the southern Jamal. p. 131-132. In: F.E. Wielgolaski and T.H. Rosswall (eds.). IBP Tundra Biome Proc. IV International meeting on the biological productivity of tundra. Leningrad, USSR. Tundra Biome Steering Committee, Stockholm. 320 p.

- Bohnsack, K.K. 1968. The distribution and abundance of the tundra arthropods in the vicinity of Pt. Barrow, Alaska. Final Report to Arctic Institute of North America; subcontracts ONR-308, ONR-321. 111 p.
- Bornebusch, C.H. 1930. The fauna of forest soil. Forstl. Forsokvais Dan. 11: 1-224.
- Bottrell, H.H. 1975. Generation time, length of life, instar duration and frequency of moulting, and their relationship to temperature in eight species of Cladocera from the river Thames, Reading. Oecologia 19: 129-140.
- Bowen, S. (ed.). 1972. US IBP Tundra Biome Symp. Univ. Washington, Seattle. 211 p.
- Briggs, M.H. 1967. Urea as a Protein Supplement. Pergamon Press, Toronto. 466 p.
- Brock, T.D. 1966. Principles of Microbial Ecology. Prentice-Hall, New Jersey. 306 p.
- Brody, S. 1964. Bioenergetics and Growth. Hafner Publ. Co., New York. 1023 p.
- Brown, W.J. (pers. comm. mimeo). 133 Metcalf, Ottawa, Ontario.
- Bruggemann, P.E. 1958. Insects and environments of the high arctic. Proc. X Int. Congr. Entomol. 1: 695-702.
- Bryk, F. 1932. Lymantriidae. p. 3-441. In: C. Aurivillius, H. Wagner, E. Strand, F. Bryk. Lepidoptorum Catalogus. Vol. XX. W. Junk, Berlin.
- Buei, K. 1967. (The relationship between the body weights of pupae of houseflies and the number of matured eggs in the ovaries.). Jpn. J. Sanit. Zool. 18: 18-20.
- Bunnell, F.L., S.F. MacLean, Jr. and J. Brown. 1975. Barrow, Alaska, USA. p. 73-124. In: T. Rosswall and O.W. Heal (eds.). Structure and Function of Tundra Ecosystems. Ecol. Bull. 20. Swedish Nat. Sci. Res. Council, Stockholm. 450 p.
- Burges, A. and F. Raw (eds.). 1967. Soil Biology. Academic Press, London. 532 p.
- Carefoot, T.H. 1973. The energy budget of the adult stage of the greater wax moth, *Galleria mellonella* (L.). Can. J. Zool. 51: 1035-1039.
- Carpelan, L. (pers. comm.). (IBP desert biome) Zoology Dept., Univ. Calif., Riverside, Calif.

- Challet, G.L. and K.K. Bohnsack. 1968. The distribution and abundance of Collembola at Pt. Barrow, Alaska. *Pedobiologia* 8: 214-222.
- Cheng, H.H. and E.J. LeRoux. 1966. Preliminary life tables and notes on mortality factors on the birch leaf miner, *Fenusa pusilla* (Lepeletier) on blue birch, *Betula caerulea grandis* Blanchard, in Quebec. *Ann. Entomol. Soc. Que.* 11: 81-104.
- Chernov, Yu. I. 1975a. A review of the trophic groups of invertebrates in typical tundra subzone of western Taimyr. p. 17-29. In: IBP Tundra Biome transl. 12. Soil invertebrates in the tundra of western Taimyr. Tundra Biome Center, Univ. Alaska. 53 p.
- Chernov, Yu. I. 1975b. Geozoological characteristics of the region of Taimyr biogeocenological station. p. 39-53. In: see above.
- Chernov, Yu. I., S.E. Anan'eva, L.L. Kuz'min, and E.P. Khajurova. 1975a. The peculiarities of vertical distribution of invertebrates in soils of tundra zone. p. 31-38. In: see above.
- Chernov, Yu. I., S.E. Anan'eva, E.P. Khajurova. 1975b. Complex of the soil invertebrates in the spot-medallion tundra of western Taimyr. p. 1-15. In: see above.
- Chernov, Yu. I. (pers. comm.). A.N. Sewerzoff Institute of Evolutionary Morphology and Animal Ecology, Leninskie prospekt 33, Moscow, USSR.
- Collins, N.J., J.H. Baker, and P.J. Tillbrook. 1975. Signy Island, maritime Antarctic. p. 345-374. In: T. Rosswall and O.W. Heal (eds.). Structure and Function of Tundra Ecosystems. *Ecol. Bull.* 20. Swedish Nat. Sci. Res. Council, Stockholm. 450 p.
- Comita, G.W. 1968. Oxygen consumption in *Diaptomus*. *Limnol. Oceanogr.* 13: 51-57.
- Corbet, P.S. 1969. Terrestrial microclimate: amelioration at high latitudes. *Science* 166: 865-866.
- Corbet, P.S. (pers. comm.). Dept. of Zoology, Univ. Canterbury, Christchurch, New Zealand.
- Corbet, P.S. and H.V. Danks. 1974. Screen temperatures during the summers 1967 and 1968 at Hazen Camp, Ellesmere Island, N.W.T. Defense Res. Board Operation Hazen 44. Ottawa. 13 p.
- Courtin, G.R. (pers. comm.). Biology Dept, Sudbury Univ., Sudbury, Ontario.
- Crescitelli, F. 1935. The respiratory metabolism of *Galleria mellonella* (bee moth) during pupal development at constant temperatures. *J. Cell. Comp. Physiol.* 6: 351-368.

- Crowe, J.H. and A.F. Cooper. 1971. Cryptobiosis. *Sci. Am.* 225: 30-36.
- Cummins, K.W. and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Ver. Theor. Angew. Limnol.* No. 18. 158 p.
- Curtis, J. 1835. Insects. p. lix-lxxx. In: J. Ross (ed.). Narrative of a second voyage in search of a north-west passage, and of a residence in the arctic regions during the years 1829-1833. Webster, London. 740 p.
- Dahl, C. 1967. Notes on arctic and subarctic Trichoceridae (Diptera: Nematocera) from Canada, Alaska, and Greenland. *Opusc. Entomol.* 32: 49-78.
- Danilov, N.N. 1972. Birds and arthropods in the tundra biogeocenosis. p. 117-121. In: F.E. Wielgolaski and T. Rosswall (eds.). IBP Tundra Biome Proc. IV International meeting on the biological productivity of tundra. Tundra Biome Steering Committee, Stockholm. 320 p.
- Danks, H.V. and J.R. Byers. 1972. Insects and arachnids of Bathurst Island, Canadian Arctic archipelago. *Can. Entomol.* 104: 81-88.
- Darlington, P.J. 1965. Biogeography of the Southern End of the World. McGraw-Hill, New York. 236 p.
- Dash, M.C. and J.B. Cragg. 1972. Selection of microfungi by Enchytraeidae (Oligochaeta) and other members of the soil fauna. *Pedobiologia* 12: 282-286.
- Dempster, J.P. 1956. The estimation of the number of individuals entering each stage during the development of one generation of an insect population. *J. Anim. Ecol.* 25: 1-5.
- Dermott, R.M. and C.G. Patterson. 1973. Determining dry weight and percentage dry matter of chironomid larvae. *Can. J. Zool.* 52: 1243-1250.
- Dickinson, C.H. and G.J.F. Pugh (eds.). 1974. Biology of Plant Litter Decomposition. Vol. 1. Academic Press, London. 416 p.
- Dobzhansky, T. 1950. Evolution in the tropics. *Amer. Scientist* 38: 208-221.
- Donner, J. 1966. (orig. german 1956). Rotifers. transl. H. Wright. Frederick Warne & Col, London. 80 p.
- Dougherty, R.W. (ed.). 1965. Physiology of Digestion in the Ruminant. Symposium. Butterworths, Washington. 480 p.

- Dowding, V.M. 1967. The function and ecological significance of the pharyngeal ridges occurring in the larvae of some cyclo-rhaphous Diptera. *Parasitology* 57: 371-388.
- Downes, J.A. 1962. What is an arctic insect? *Can. Entomol.* 94: 143-162.
- Downes, J.A. 1964. Arctic insects and their environment. *Can. Entomol.* 96: 279-307.
- Downes, J.A. 1965. Adaptations of arctic insects to their environments. *Annu. Rev. Entomol.* 10: 257-274.
- Downes, J.A. 1966. The Lepidoptera of Greenland; some geographic considerations. *Can. Entomol.* 98: 1135-1144.
- Downes, J.A. 1970. The feeding and mating behavior of the specialized Empidinae (Diptera); observations on four species of *Rhamphomyia* in the high arctic, and a general discussion. *Can. Entomol.* 102: 769-791.
- Downes, J.A. (pers. comm.). Lepidoptera-Trichoptera section, Biosystematics Research Institute, K.S. Neatby Bldg., Ottawa, Ontario. K1A 0C6
- Edgar, W.D. 1971a. Seasonal weight changes, age structure, natality, and mortality in the wolf spider *Pardosa lugubris* Walck. in central Scotland. *Oikos* 22: 84-92.
- Edgar, W.D. 1971b. Aspects of the ecological energetics of the wolf spider *Pardosa (Lycosa) lugubris* (Walckenaer). *Oecologia* 7: 136-154.
- Edmondson, W.T. 1968. A graphical model for evaluating the use of the egg ratio for measuring birth and death rates. *Oecologia* 1: 1-37.
- Edwards, C.A. and K.E. Fletcher. 1971. A comparison of extraction methods for terrestrial arthropods. p. 150-185. In: J. Phillipson (ed.). *Quantitative Soil Ecology*, IBP Handbook No. 18. Blackwell, London. 297 p.
- Edwards, C.A., D.E. Reichle, and D.A. Crossley, Jr. 1970. The role of soil invertebrates in turnover of organic matter and nutrients. *Ecol. Stud.* 1: 147-172.
- Embree, D.G. 1956. The population dynamics of the winter moth in Nova Scotia, 1954-1962. *Mem. Entomol. Soc. Can.* No. 46. 57 p.
- Englemann, M.D. 1961. The role of soil arthropods in the energetics of an old field community. *Ecol. Monogr.* 31: 221-238.

- Englemann, M.D. 1966. Energetics, terrestrial field studies, and animal productivity. *Adv. Ecol. Res.* 3: 73-115.
- Englemann, M.D. 1968. The role of soil arthropods in community energetics. *Am. Zool.* 8: 61-69.
- Fenchel, T. 1974. The quantitative importance of the benthic microfauna of an arctic tundra pond. *Hydrobiologia* 46: 445-464.
- Ferguson, D.A. (pers. comm.). Lepidoptera section, Smithsonian Institution, Washington, D.C. 20560.
- Fittkau, E.J. and H. Klinge. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* 5: 1-14.
- Flatt, W.P. and P.W. Moe. 1969. Energy requirements. p. 269-290. In: E.S.E. Hafez and I.A. Dyer (eds.). *Animal Growth and Nutrition*. Lea & Fibiger, Philadelphia. 402 p.
- Flower-Ellis, J. (ed.). 1973. IBP Swedish Tundra Biome Project. Tech. Rep. 16. Swedish Nat. Sci. Res. Council, Stockholm. 212 p.
- Forbes, S.A. 1887. The lake as a microcosm. *Bull. Sc. A. Peoria*. Reprinted in *Ill. Nat. Hist. Surv. Bull.* 15: 537-550. (1925).
- Gaede, M. 1934. *Lymantria*. p. 100-102. In: A. Seitz. *The Macrolepidoptera of the World*. Suppl. to Vol. 2. A. Kernan, Stuttgart. 315 p.
- Gascoigne, J.A. and M.M. Gascoigne. 1960. *Biological Degradation of Cellulose*. Butterworths, London. 246 p.
- Gibson, A. 1922. The Lepidoptera collected by the Canadian Arctic Expedition, 1913-18. In: Report of the Canadian Arctic Expedition, 1913-18. Vol. 3.I. King's Printer, Ottawa. 58 p.
- Goldschmidt, R. 1934. *Lymantria*. *Bibliogr. Genet.* 11: 1-186.
- Golley, F.B. 1968. Secondary productivity in terrestrial communities. *Am. Zool.* 8: 53-59.
- Golley, F.B. and J.B. Gentry. 1964. Bioenergetics of the southern harvester ant, *Pogonomyrmex badius*. *Ecology* 45: 217-225.
- Goulden, C.H. 1952. *Methods of Statistical Analysis*. Wiley, New York. 467 p.
- Gressitt, J.L., R.E. Leech, and K.A. Wise. 1963. Entomological investigations in Antarctica. *Pac. Insects* 5: 287-304.

- Haag, R.W. 1974. Nutrient limitations to plant production in two tundra communities. *Can. J. Bot.* 52: 103-116.
- Hadley, M. 1971. Pupation and fecundity of *Molophilus ater* Meigen (Diptera: Tipulidae) in relation to larval weight. *Oecologia* 7: 164-169.
- Hale, W.G. 1967. Collembola. p. 397-412. In: A. Burges and F. Raw (eds.). *Soil Biology*. Academic Press, London. 532 p.
- Hallas, T.E. and G.W. Yeates. 1972. Tardigrada of the soil and litter of a Danish beech forest. *Pedobiologia* 12: 287-304.
- Hanegan, J.L. and J.E. Heath. 1970. Mechanisms for the control of body temperature in the moth, *Hyalophora cecropia*. *J. Exp. Biol.* 53: 611-628.
- Harcourt, D.G. 1966. Major factors in survival of the immature stages of *Pieris rapae* (L.). *Can. Entomol.* 98: 653-662.
- Harcourt, D.G. 1969. The development and use of life tables in the study of natural insect populations. *Annu. Rev. Entomol.* 14: 175-196.
- Haukioja, E. 1973. Weight development, consumption, and egestion of *Dineura virididorsata* (Hym. Tenthredinidae) larvae. *Rep. Devo Subarctic Res. Stat.* 10: 9-13.
- Haukioja, E. 1976. Faunal-plant interactions in tundra: the role of invertebrate herbivory. (in press). In: J.J. Moore (ed.). *Tundra: Comparative Analysis of Ecosystems*. Cambridge Univ. Press, Cambridge.
- Haukioja, E., S. Koponen, and H. Ojala. 1973. Local differences in birch leaf consumption by invertebrates in northern Norway and Finland. *Rep. Kevo-Subarctic Res. Stat.* 10: 29-33.
- Heal, O.W. 1965. Observations on testate amoebae (Protozoa: Rhizopoda) from Signy Island, South Orkney Islands. *Br. Antarct. Surv. Bull.* 6: 43-47.
- Heal, O.W. 1967. Quantitative feeding studies on soil amoebae. p. 120-126. In: O. Graff and J. Satchell (eds.). *Progress in Soil Biology*. Braunschweig, Wieweg. 656 p.
- Heal, O.W. 1971. Protozoa. p. 51-71. In: J. Phillipson (ed.). *Quantitative Soil Ecology*, IBP Handbook No. 18. Blackwell, London. 297 p.
- Heal, O.W. H.E. Jones, and J.B. Whittaker. 1975. Moor House, U.K. p. 295-320. In: T. Rosswall and O.W. Heal (eds.). *Structure and Function of Tundra Ecosystems*. *Ecol. Bull.* 20. Swedish Nat. Sci. Res. Council, Stockholm. 450 p.

- Heal, O.W. and S.F. MacLean, Jr. 1975. Comparative productivity in ecosystems - Secondary productivity. Concepts in Ecology 38: 25-32.
- Healey, I.N. 1967. The population metabolism of *Onychiurus procam-patus* Gisin (Collembola). p. 127-137. In: O. Graff and J. Satchell (eds.). Progress in Soil Biology. Braunschweig, Wieweg. 656 p.
- Healey, I.N. 1971. Apterygotes, pauropods, and symphylans. p. 209-232. In: J. Phillipson (ed.). Methods of Study in Quantitative Soil Ecology: Population, Production, and Energy Flow. Blackwells, London. 297 p.
- Heinrich, B. 1973. The energetics of the bumblebee. Sci. Amer. 228: 96-102.
- Heinrich, B. (pers. comm.). Dept. of Entomology, Univ. California, Berkeley.
- Hobbie, J. 1972. Carbon flux through a tundra pond ecosystem at Barrow, Alaska. p. 206-208. In: S. Bowen (ed.). US IBP Tundra Biome Symp. Univ. Washington, Seattle. 211 p.
- Hobbie, J.E. 1973. Arctic limnology: a review. p. 127-168. In: M.E. Britton (ed.). Alaska Arctic Tundra. Arctic Institute of North America Tech. paper No. 25. Montreal.
- Hocking, B. 1953. The intrinsic range and speed of flight of insects. Trans. R. Entomol. Soc. Lond. Ser. B. 104: 223-345.
- Hodkinson, I.D. 1973. The population dynamics and host plant interactions of *Strophingia ericae* (Curt.) (Homoptera: Psylloidea). J. Anim. Ecol. 42: 565-583.
- Hoffmann, K.-H. 1976. Organic body constituents of *Protophormia terrae-novae* (Dipt.) from Spitsbergen compared with flies from a laboratory stock. Oecologia 23: 13-16.
- Hofsvang, T. 1973. Energy flow in *Tipula excisa* Schum. (Diptera, Tipulidae) in a high mountain area, Finse, south Norway. Norw. J. Zool. 21: 7-16.
- Holding, A.J., O.W. Heal, S.F. MacLean, and P.W. Flanagan (eds.). 1974. Soil Organisms and Decomposition in Tundra, Proc. IBP working groups meeting. Tundra Biome Steering Committee, Stockholm. 398 p.
- Hopkins, D.M. 1974. Seminar on Paleogeography and climatic history. Univ. Alberta, Edmonton.

- Hubert, B. 1972. Productivity of muskox. p. 272-280. In: L.C. Bliss (ed.). Devon Island IBP Project, High Arctic Ecosystem. 413 p.
- Hughes, D.E. and A.H. Rose (eds.). 1971. Microbes and Biological Productivity. Soc. for General Microbiology, Symp. 21. Cambridge U. Press. 378 p.
- Huhta, V. and A. Koskenniemi. 1975. Numbers, biomass and community respiration of soil invertebrates in spruce forests at two latitudes in Finland. An. Zool. Fenn. 12: 164-182.
- Hurd, P.D. and E.E. Lindquist. 1958. Analysis of soil invertebrate samples from Barrow, Alaska. Final Report, Arctic Institute of North America, Washington. ONR-173 and ONR-193. 24 p.
- Hussel, D.J.T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317-364.
- Ivleyva, I.V. 1953. Growth and reproduction of the potworm (*Enchytraeus albidus* Henlé). Zool. Zh. 32: 394-404.
- Jacobson, L.A. 1970. Laboratory ecology of the red-backed cutworm, *Euxoa ochrogaster* (Lepidoptera: Noctuidae). Can. Entomol. 102: 85-89.
- Janzen, D.H. and C.M. Pond. 1975. A comparison, by sweep sampling, of the arthropod fauna of secondary vegetation in Michigan, England, and Costa Rica. Trans. Roy. Ent. Soc. Lond. 127: 33-50.
- Jenkin, J.F. 1975. Macquarie Island, Subantarctic. p. 375-397. In: T. Rosswall and O.W. Heal (eds.). Structure and Function of Tundra Ecosystems. Ecol. Bull. 20. Swedish Nat. Sci. Res. Council, Stockholm. 450 p.
- Johannes, R.E. and S. Masako. 1966. Composition and nutritive value of fecal pellets of a marine crustacean. Limnol. Oceanogr. 11: 191-197.
- Kajak, A. 1971. Productivity investigation of two types of meadows in the Vistula Valley. IX. Production and consumption of field layer spiders. Ekol. Polska XIX (15): 197-211.
- Kauri, H., T. Moldung, and T. Solhøy. 1969. Turnbull and Nicholl's 'Quick Trap' for acquiring standing crop of invertebrates in high mountain grassland communities at Hardangervidda, South Norway. Norw. J. Entomol. 19: 99-108.
- Keister, M. and J. Buck. 1974. Respiration: some exogenous and endogenous effects on rate of respiration. p. 469-509. In: M. Rockstein (ed.). The Physiology of Insecta. Vol. VI. Academic Press, New York. 548 p.
- Kennedy, L.L. (pers. comm.) Microbiology section, Botany Dept., Univ. Alberta.
- Kessler, A. 1971. Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia 8: 93-109.

- Kevan, P.G. 1970. High Arctic insect-flower relations: the inter-relationships of arthropods and flowers at Lake Hazen, Ellesmere Island, N.W.T., Canada. PhD thesis. Entomology Dept., Univ. Alberta. 399 p.
- Kevan, P.G. 1972. Insect pollination of high arctic flowers. *J. Ecol.* 60: 831-847.
- Kevan, P.G. 1973. Flowers, insects, and pollination ecology in the Canadian high Arctic. *Polar Record.* 16: 667-674.
- Kevan, P.G. 1975. Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. *Science.* 189: 723-726.
- Kevan, P.G. and O.K. Kevan. 1970. Collembola as pollen feeders and flower visitors, with observations from the high Arctic. *Quaest. ent.* 6: 311-326.
- Kevan, P.G. and J.B. Shorthouse. 1970. Behavioural thermoregulation by high arctic butterflies. *Arctic* 23: 268-279.
- Kleiber, M. 1961. *The Fire of Life; an Introduction to Animal Energetics.* John Wiley & Sons, New York. 454 p.
- Knight, F.B. 1959. Partial life tables for the black hills beetle. *J. Econ. Entomol.* 52: 1200-1202.
- Kowal, N.E. and D.A. Crossley. 1971. The ingestion rates of microarthropods in pine mor, estimated with radioactive calcium. *Ecology* 52: 444-452.
- Kozhanchikov, I.B. 1950. (Orgyids of the USSR). *Zool. Inst. Akad. Nauk SSSR, Moscow (N.S.)* 42. Insects--Lepidoptera 12. 582. 296 fig.
- Kozlovsky, D.G. 1968. A critical evaluation of the trophic level concept. I. Ecological efficiencies. *Ecology* 49:48-59.
- Krebs, C.J. 1972. *Ecology, the Experimental Analysis of Distribution and Abundance.* Harper and Rowe, San Francisco. 694 p.
- Lasker, R. and A.C. Giese. 1956. Cellulose digestion by the silverfish *Ctenolepisma lineata*. *J. Exp. Biol.* 33: 542-553.
- Lawton, J.H. 1971. Ecological energetics studies on larvae of the damselfly *Pyrrosoma nymphula* (Sulzer) (Odonata: Zygoptera). *J. Anim. Ecol.* 40: 385-423.
- Laybourn, J. 1976. Energy budgets for *Stentor coeruleus* Ehrenberg (Ciliophora). *Oecologia* 22: 431-437.

- Learner, M.J. 1972. Laboratory studies on the life-histories of four enchytraeid worms (Oligochaeta) which inhabit sewage percolating filters. *Ann. appl. Biol.* 70: 251-266.
- Leech, R.E. 1966. The spiders (Araneida) of Hazen Camp, 81°49'N, 71°18'W. *Quaest. Entomol.* 2: 153-212.
- Leech, R.E. (pers. comm.) Research Secretariat, Alberta Environment, Oxbridge Place, 9820 - 106 St., Edmonton, Alberta. T5K 2J6
- Leech, R.E. and J.K. Ryan. 1974. Notes on Canadian Arctic spiders (Araneida), mainly from Devon Island, N.W.T. *Can. Entomol.* 104: 1787-1791.
- Lindemann, R.L. 1942. The trophic dynamic aspect of ecology. *Ecology* 23: 399-417.
- Luff, M.L., B.J. Selman, and G.N. Foster. 1974. The Coleoptera of Castle Eden dene. *Trans. Nat. Hist. Soc. Northumberland. Durham Newcastle Upon Tyne.* Vol. 41: 179-193.
- Luxton, M. 1972. Studies on the oribatid mites of a Danish beech wood soil. I. Nutritional biology. *Pedobiologia* 12: 434-463.
- MacArthur, R.H. 1972. *Geographical Ecology: Patterns in the Distribution of Species.* Harper & Rowe, New York. 269 p.
- MacArthur, R.H. and E.O. Wilson. 1967. *The Theory of Island Biogeography.* Princeton Univ. Press, Princeton. 203 p.
- Macfadyen, A. 1963a. The contribution of the microfauna to total soil metabolism. p. 3-17. In: J. Doeksen, and J. van der Drift (eds.). *Soil Organisms.* North Holland Publ. Co., Amsterdam.
- Macfadyen, A. 1963b. *Animal Ecology, Aims and Methods.* Pitman & Sons, London. 264 p.
- MacKay, M.R. and J.R. Downes. 1969. Arctic Olethreutinae (Lepidoptera: Tortricidae). *Can. Entomol.* 101: 1048-1053.
- MacLean, S.F. 1973. The life cycle and growth energetics of *Pedicia hanna antennata* Alex. (Diptera: Tipulidae), an arctic crane fly. *Oikos* 24: 436-443.
- MacLean, S.F. 1975. Ecological adaptations of tundra invertebrates. p. 269-300. In: F.J. Vernberg (ed.). *Physiological Adaptation to the Environment.* Intext Educational Publ., New York. 576 p.
- MacLean, S.F. Jr. 1976. Populations, biomass, and energetic relationships of tundra invertebrates. (in press). In: J.J. Moore (ed.). *Tundra: Comparative Analysis of Ecosystems.* Cambridge Univ. Press, Cambridge.

- MacLean, S.F. (pers. comm.) Institute of Arctic Biology, Univ. Alaska, Fairbanks, Alaska.
- Mani, M.S. 1968. Ecology and Biogeography of High Altitude Insects. Junk, the Hague. 527 p.
- Manly, B.J.F. 1974. Estimation of stage specific survival rates and other parameters for insect populations developing through several stages. *Oecologia* 15: 277-286.
- Mason, W.R.M. (pers. comm.). Hymenoptera Section, Biosystematics Research Institute, Ottawa, Ontario. KIA OC6
- McAlpine, J.F. 1964. Arthropods of the bleakest barren lands: composition and distribution of the arthropod fauna of the northwestern Queen Elizabeth Islands. *Can. Entomol.* 96: 127-219.
- McAlpine, J.F. 1965. Insects and related terrestrial invertebrates of Ellef Ringnes Island. *Arctic* 18: 73-103.
- McBrayer, J.F. and D.E. Reichle. 1971. Trophic structure and feeding rates of forest soil invertebrate populations. *Oikos* 22: 381-388.
- McCauley, V.J.E. 1975. Life tables for some natural populations of Chironomidae (Diptera) in a *Typha* marsh. PhD thesis. Entomology Dept., Univ. Alberta. 199 p.
- McGuffin, W.C. (pers. comm.). Head, Lepidoptera-Trichoptera section, Biosystematics Research Institute, Ottawa, Ontario. KIA OC6.
- Meats, A. 1975. The developmental dynamics of *Tipula paludosa* and the relation of climate to its growth pattern, flight season and geographical distribution. *Oecologia* 19: 117-128.
- Milliron, H.E. and D.R. Oliver. 1966. Bumblebees from northern Ellesmere Island, with observations on usurpation by *Megabombus hyperboreus* (Schoenh.) (Hymenoptera: Apidae). *Can. Entomol.* 98: 207-213.
- Minns, C.K. 1977. Limnology of some lakes on the Truelove Lowland. (in press). In: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Moon, B.J. and T.H. Carefoot. 1972. The energy requirements of metamorphosis of the greater wax moth, *Galleria mellanella* (L.). *Can. J. Zool.* 50: 67-75.
- Morris, R.E. and G.A. Miller. 1954. The development of life tables for the spruce budworm. *Can. J. Zool.* 32:283-301.

- Moulder, B.C., D.E. Reichle, and S.E. Auerbach. 1970. Significance of spider predation in the energy dynamics of forest floor arthropod communities. Oak Ridge National Lab., Tennessee. 1970 p.
- Muc, M. 1977. Ecology and primary production of raised beach communities, Truelove Lowland. (in press). In: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Mukerji, M.K. and J.C. Guppy. 1970. A quantitative study of food consumption and growth in *Pseudaletia unipuncta* (Lepidoptera: Noctuidae). Can. Entomol. 102: 1179-1188.
- Mulvey, R.H. 1963. Some soil-inhabiting, freshwater, and plant parasitic nematodes from the Canadian Arctic and Alaska. Arctic 16: 202-204.
- Mundie, J.H. 1956. Emergence traps for aquatic insects. Mitt. Int. Vert. Theor. Angew. Limnol. 7. 13 p.
- Mundie, J.H. 1973. (oral presentation). Aquatic fauna, sampling, and relation to environmental quality. Entomol. Soc. Can. 23 Meeting, Banff, Alberta.
- Nelson, L. 1977. Growth and survival characteristics of three arctic soil bacteria. (in press). In: L.C. Bliss (ed.) Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta press, Alberta. c.a. 850 p.
- Nelson, J.M. 1971. The invertebrates of an area of pennine moorland within the Moor House Nature Reserve in northern England. Trans. Soc. Brit. Entomol. 19: 173-235.
- Nielsen, C.O. 1951. Respiratory metabolism of some populations of enchytraeid worms and free living nematodes. Oikos 12: 17-35.
- Nielsen, C.O. 1952. Studies on the Enchytraeidae. 1. A technique for extracting Enchytraeidae from soil samples. Oikos 4: 187-196.
- Nielsen, C.O. 1962. Carbohydrases in soil and litter invertebrates. Oikos 13: 200-215.
- Nielsen, C.O. 1967. Nematoda. p. 197-211. In: A. Burges and F. Raw (eds.). Soil Biology. Academic Press, London. 532 p.
- Nuriminen, M. 1973. Enchytraeidae (Oligochaeta) from the arctic archipelago of Canada. Ann. Zool. Fenn. 10: 403-411.
- O'Connor, F.B. 1955. Extraction of enchytraeid worms from a coniferous forest soil. Nature (Lond.) 1975: 815-816.

- O'Connor, F.B. 1962. The extraction of Enchytraeidae from soil. p. 279-285. In: P.W. Murphy (ed.). Progress in Soil Zoology. Butterworths, London. 398 p.
- O'Connor, F.B. 1967. The Enchytraeidae. In: A. Burges and F. Raw (eds.). Soil Biology. Academic Press, London. 532 p.
- O'Connor, F.B. 1971. The enchytraeids. p. 83-106. In: J. Phillipson (ed.). Methods of Study in Quantitative Soil Ecology: Population, Production, and Energy Flow. IBP Handbook No. 18. Blackwells, London. 297 p.
- Odum, E.P. 1968. Energy flow in ecosystems: a historical review. Am. Zool. 8: 11-18.
- Odum, E.P. 1971. Fundamentals of Ecology. W.B. Saunders & Co., Toronto. 574 p.
- Odum, H.T. 1956. Efficiencies, size of organisms and community structure. Ecology 37: 592-597.
- Ohshima, Y. and E. Asahina. 1971. Frost resistance in an alpine moth *Byrdia rossi* (Diasetsuzana: Lymantriidae). Low Temp. Sci. Ser. B. Biol. Sci. 29: 121-123.
- Olechowicz, E. 1971. Productivity investigation of two types of meadows in the Vistula Valley. VIII. The number of emerged Diptera and their elimination. Ekol. Polska 19: 183-195.
- Oliver, D.R. 1963. Entomological studies in the Lake Hazen area, Ellesmere Island, including lists of species of Arachnida, Collembola, and Insects. Arctic 16: 175-180.
- Oliver, D.R. 1968. Adaptations of arctic Chironomidae. Ann. Zool. Fenn. 5: 111-118.
- Oliver, D.R. (pers. comm.) Diptera section, Biosystematics Research Institute, K.S. Neatby Bldg, Ottawa. K1A 0C6
- Paris, O.H. 1967. The function of soil fauna in grassland ecosystems. p. 331-360. In: R.L. Dix and R.G. Beidleman (eds.). The Grassland Ecosystem: a Preliminary Synthesis. Range Sci. Dept. Sci. Ser. No. 2. Colorado State Univ., Fort Collins.
- Pattie, D.L. 1972. Preliminary bioenergetic and population level studies in high arctic birds. p. 281-292. In: L.C. Bliss (ed.). Devon Island IBP Project, High Arctic Ecosystem. Univ. Alberta Press, Alberta. 413 p.
- Pattie, D.L. 1974. (unpubl. report). Truelove Lowland Birds. oral, 1 table. IBP Project Meeting, Kananaskis Res. Stat., Alberta.

- Pattie, D.L. 1977. Vertebrate species list. (in press). Appendix in: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Pattie, D.L. (pers. comm.). Biology Dept., Northern Alberta Institute of Technology, Edmonton, Alberta.
- Pearl, R., T. Park, and J.R. Miner. 1941. Experimental studies on the duration of life. XVI. Life tables for the flour beetle *Tribolium confusum* Duval. Am. Nat. 75: 5-19.
- Pennak, R.W. 1953. Fresh-water Invertebrates of the United States. Chapt. 17: Copepoda. Ronald Press Co., New York. 769 p.
- Petruscewicz, K. and A. Macfadyen. 1970. Productivity of Terrestrial Animals, Principles and Methods. IBP Handbook No. 13. Blackwells, London. 190 p.
- Petrides, G.A. and W.G. Swank. 1966. Estimating the productivity and energy relations of an African elephant population. Vol. 1: 831-842. Proc. IX Int. Grass. Congr., San Paulo, Brazil. 1974 p.
- Phillips, K. (pers. Comm.) Alaska Lepidoptera Survey. Institute of Arctic Biology, Univ. Alaska, College, Alaska. 99701.
- Phillipson, J. 1960. A contribution to the feeding biology of *Mitopus morio* (F.) (Phalangida). J. Anim. Ecol. 29: 35-43.
- Phillipson, J. 1961. Respirometry and study of energy turnover in natural ecosystems, with particular reference to the harvest spider. Oikos 13: 311-322.
- Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. Oikos 15: 130-139.
- Phillipson, J. 1966. Ecological Energetics. Edward Arnold, London. 57 p.
- Phillipson, J. 1971. Methods of Study in Quantitative Soil Ecology: Population, Production, and Energy Flow. IBP Handbook No. 18. Blackwell, Oxford. 297 p.
- Porsild, A.E. 1964. Illustrated Flora of the Canadian Arctic Archipelago. Nat. Mus. Can. Bull. 146. Queen's Printer, Ottawa. 218 p.
- Procter, D.L.C. 1977a. Invertebrate respiration on the Truelove Lowland. (in press). In: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.

- Procter, D.L.C. 1977b. Nematode densities and production on the Truelove Lowland. (in press). In: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Prosser, G.L. 1973. Comparative Animal Physiology. W.B. Saunders Co., Toronto. 966 p.
- Reichle, D.E. 1968. Relation of body size to food intake, oxygen consumption, and trace element metabolism in forest floor arthropods. Ecology 49: 538-542.
- Reichle, D.E., R.A. Goldstein, R.I. VanHook, Jr., and G.J. Dodson. 1973. Analysis of insect consumption in a forest canopy. Ecology 54: 1076-1084.
- Reynoldson, T.B. 1939. On the life-history and ecology of *Lumbricillus lineatus* Mull. (Oligochaeta). Ann. Appl. Biol. 26: 782-799.
- Reynoldson, T.B. 1943. A comparative account of the life cycles of *Lumbricillus lineatus* Mull. and *Enchytraeus albidus* Henlé in relation to temperature. Ann. Appl. Biol. 30: 60-66.
- Richards, K.W. 1973. Biology of *Bombus polaris* Curtis and *B. hyperboreus* Schoenherr at Lake Hazen, Northwest Territories (Hymenoptera: Bombini). Quaest. Entomol. 9: 115-157.
- Richards, W.R. 1963. The Aphididae of the Canadian arctic. Can. Entomol. 95: 449-464.
- Richards, W.R. 1964. The scale insects of the Canadian arctic (Hymenoptera: Coccoidea). Can. Entomol. 96: 1457-1462.
- Richardson, D.H. 1977. Lichen species list. (in press). Appendix in: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Richman, S. 1958. The transformation of energy by *Daphnia pulex*. Ecol. Monogr. 28: 273-291.
- Riegert, P.W. and J.L. Varley. 1973. Above-ground Invertebrates: II. Population dynamics and biomass production of grasshoppers. IBP Tech. Rep. 16. Univ. Saskatchewan. 134 p.
- Riegert, P.W., J.L. Varley, and B.C. Dunn. 1974. Above-ground Invertebrates: IV. Populations and energetics of spiders. CCIBP Matador Proj. Tech. Rep. 57. Univ. Saskatchewan. 76 p.
- Roff, J.C. 1973. Oxygen consumption of *Limnocalanus macrurus* Sars (Calanoida, Copepoda) in relation to environmental conditions. Can. J. Zool. 51: 877-885.

- Rogers, L., R. Lavigne, and J.L. Miller. 1972. Bioenergetics of the western harvester ant in the short grass plains ecosystem. *Environ. Entomol.* 1: 763-768.
- Rosswall, T. and O.W. Heal (eds.). 1975. Structure and Function of Tundra Ecosystems. *Ecol. Bull.* 20. Swedish Nat. Sci. Res. Council, Stockholm. 450 p.
- Ryan, J.K. 1972. Devon Island Invertebrate research. p. 293-314. In: L.C. Bliss (ed.). Devon Island IBP Project, High Arctic Ecosystem. Univ. Alberta Press, Alberta. 413 p.
- Ryan, J.K. 1973. A quantitative feeding study of *Pieris rapae* L. (Lepidoptera, Pieridae) on *Brassica oleracea* L. (abst. only). *Proc. 23 Annu. Entomol. Soc., Banff, Alberta.*
- Ryan, J.K. 1976. Comparison of invertebrate species lists from IBP tundra sites. (in press). In: J.J. Moore (ed.). Tundra: Comparative Analysis of Ecosystems. Cambridge Univ. Press, Cambridge.
- Ryan, J.K. 1977a. Invertebrate species list. (in press). Appendix in: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Ryan, J.K. 1977b. Synthesis of energy flows and populations dynamics of Truelove Lowland invertebrates. (in press). In: L.C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Saville, D.B.O. 1972. Arctic Adaptations in Plants. Monogr. No. 6. Can. Dept. Agri. Queen's Printer, Ottawa. 81 p.
- Schaeffer, P.W. (pers. comm.) formerly: Entomology Dept., Univ. Maine, Orono, Maine. 04473.
- Scholander, P.F., W.F. Flagg, V. Walters and L. Irving. 1953. Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.* 26: 67-92.
- Schramm, U. 1972. Temperature-food interaction in herbivorous insects. *Oecologia* 9: 399-402.
- Schroeder, L.A. 1971. Energy budget of larvae of *Hyalophora-Cecropia* (Lepidoptera) fed *Acer-Negundo*. *Oikos* 22: 256-259.
- Schroeder, L.A. 1972. Energy budget of cecropia moths, *Platysamia cecropia* (L.) (Lepidoptera, Saturniidae), fed lilac leaves. *Ann. Entomol. Soc. Am.* 65: 367-372.
- Schroeder, L.A. 1973. Energy budget of the larvae of the moth *Pachysphinx modesta*. *Oikos* 24: 278-281.

- Schroder, L.A. and D.G. Dunlap. 1970. Respiration of cecropia moth (*Hyalophora cecropia* L.) larvae. *Compr. Biochem. Physiol.* 35: 953-957.
- SCIBP. 1974. Quantities, Units and Symbols. International Council of Scientific Unions, London. 64 p.
- Siu, R.G.H. 1955. Microbial Decomposition of Cellulose, with Special Reference to Cotton Textiles. Reinhold, New York. 531 p.
- Slobodkin, L.B. 1962. Energy in animal ecology. *Adv. Ecol. Res.* 1: 69-101.
- Smalley, A.E. 1960. Energy flow of a salt marsh grasshopper population. *Ecology* 41: 672-677.
- Sohlenius, B. 1968. Studies on the interactions between *Mesodiplogaster* sp. and other rhabditid nematodes and a protozoan. *Pedobiologia* 8: 340-344.
- Solhøy, T. 1972. Quantitative invertebrate studies in mountain communities at Hardangervidda, South Norway. *Norw. J. Entomol.* 19: 99-108.
- SooHoo, C.F. and G. Fraenkel. 1966. The consumption, digestion, and utilization of food plants by polyphagous insect, *Prodenia eridania* (Cramer). *J. Insect Physiol.* 12: 711-730.
- Southwood, T.R.E. 1966. Ecological Methods, with Particular Reference to the Study of Insect Populations. Chapman and Hall, London. 391 p.
- Spector, W.S. (ed.). 1956. Handbook of Biological Data. W.B. Saunders Co., Philadelphia. 584 p.
- Spinage, C.A. 1972. African ungulate life tables. *Ecology* 53: 645-652.
- Stark, R.W. 1958. Life tables for the lodgepole needle miner *Recurvaria starki* Free. *Proc. X Int. Congr. Entomol.* (Montreal, 1956) 4: 151-162.
- Steele, J.H. (ed.). 1970. Marine Food Chains. Univ. Calif. Press, Berkeley. 552 p.
- Steigen, A.L., T. Solhøy, and G. Gyllenberg. 1975. Energy budget of a population of adult *Carabodes labrinthicus* (Mich.) (Acari, Oribatei). *Norw. J. Entomol.* 22: 59-61.
- Stone, A., C.W. Sabrosky, W.W. Wirth, R.H. Foote, J.R. Coulson. 1965. A Catalogue of the Diptera of America North of Mexico. US govt. printing office, Washington. 1696 p.

- Stout, J.D. 1973. The relationship between protozoan populations and biological activity in soils. *Am. Zool.* 13: 193-202.
- Stout, J.D. and O.W. Heal. 1967. Protozoa. p. 149-195. In: A. Burges and F. Raw (eds.). *Soil Biology*. Academic Press, London. 532 p.
- Strandtmann, R.W. 1971. The eupodid mites of Alaska. *Pac. Insects* 13: 75-118.
- Stutz, R.C. 1972. Nitrogen fixation studies on Devon Island. p. 252-256. In: L.C. Bliss (ed.). *Devon Island IBP Project, High Arctic Ecosystem*. Univ. Alberta Press, Alberta. 413 p.
- Stutz, R.C. 1974 (unpubl. report). Nitrogen fixation. 6 p. IBP project meeting, Kananaskis Res. Station, Alberta.
- Svoboda, J. 1977. Ecology and primary production of raised beach communities, Truelove Lowland. (in press). In: L.C. Bliss (ed.). *Truelove Lowland, Devon Island, Canada: High Arctic Ecosystem*. Univ. Alberta Press, Alberta. c.a. 850 p.
- Taylor, P. 1974. Summer population and food ecology of jaegers and snowy owls on Bathurst Island, N.W.T. M.Sc. thesis. Zoology Dept. Univ. Alberta. 168 p.
- Tillbrook, P.J. 1967. The terrestrial invertebrate fauna of the maritime Antarctic. *Phil. Trans. R. Soc. Lond. Ser. B.* 262: 267-278.
- Tillbrook, P.J. 1970. The terrestrial environment and invertebrate fauna of the maritime Antarctic. p. 886-896. In: M.W. Holdgate (ed.). *Antarctic Ecology, Vol. 2*. Academic Press, New York. 998 p.
- VanDerDrift, J. 1951. Analysis of the animal community in a beech forest floor. *Tijdschr. Entomol.* 94: 1-168.
- VanHook, R.I., Jr. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. *Ecol. Monogr.* 41: 1-26.
- Verduin, J. 1972. Caloric Content and available energy in plant matter. *Ecology* 53: 982.
- Vitt, D.H. 1977. Moss species list. (in press). Appendix in: L.C. Bliss (ed.). *Truelove Lowland, Devon Island: High Arctic Ecosystem*. Univ. Alberta Press, Alberta. c.a. 850 p.
- Waldbauer, G.P. 1968. The consumption and utilization of food by insects. *Adv. Insect Physiol.* 5: 229-288.
- Wallwork, J.A. 1967. Acari. p. 363-395. In: A. Burges and F. Raw (eds.). *Soil Biology*. Academic Press, London. 532 p.

- Waters, T.F. 1969. The turnover ratio in production ecology of freshwater invertebrates. *Am. Nat.* 103: 173-185.
- Webb, N.R. and G.W. Elmes. 1972. Energy budget for adult *Steganacarus magnus* (Acari). *Oikos* 23: 359-365.
- Welch, H.E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. *Ecology* 49: 755-759.
- Welch, H.E. 1973. Emergence of Chironomidae (Diptera) from Char Lake, Resolute, N.W.T. *Can. J. Zool.* 51: 1113-1123.
- Whittaker, J.B. 1965. Auchenorrhyncha (Homoptera) of the Moor House National Nature Reserve, Westmorland, with notes on *Macrosteles alpinus* (Zett.), a species new to Britain. *Entomol. Mon. Mag.* 100: 168-171.
- Whittaker, J.B. 1973. (unpubl. report). Report on Moor House IBP invertebrate projects. August 1973. Univ. Alaska, Fairbanks, Alaska.
- Whittaker, J.B. (pers. comm.) Dept of Biology, Univ. Lancaster, Lancaster, U.K.
- Whitfield, D.W.A. 1977. Energy budgets and ecological efficiencies on the Truelove Lowland. (in press). In: L.C. Bliss (ed.). Truelove Lowland, Devon Island: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Widden, P. 1977. Microbiology and decomposition on the Truelove Lowland. (in press). In: L.C. Bliss (ed.). Truelove Lowland, Devon Island: High Arctic Ecosystem. Univ. Alberta Press, Alberta. c.a. 850 p.
- Wiegert, R.B. 1974. A theory based on realistic, general equations of population growth. *Science* 185: 539-542.
- Wielgolaski, F.E. and T. Rosswall (eds.). 1972. IBP Tundra Biome. Proc. IV Int. Meeting on the Biological Productivity of Tundra, Leningrad, USSR. Tundra Biome Steering Committee, Stockholm. 320 p.
- Willard, J.R. 1972. Soil Invertebrates: I. Methods of sampling and extraction. IBP Tech. Rep. 7. Univ. Saskatchewan. 40 p.
- Willard, J.R. 1973a. Soil Invertebrates: III. Collembola and minor insects: populations and biomass. IBP Tech. Rep. 16. Univ. Saskatchewan. 75 p.
- Willard, J.R. 1973b. Soil Invertebrates: IV. Acarina, minor Arachnida, and Chilopoda: populations and biomass. IBP Tech. Rep. 20. Univ. Saskatchewan. 75 p.

Willard, J.R. 1973c. Soil Invertebrates: VII. Enchytraeidae (Annelida: Oligochaeta): populations and biomass. IBP Tech. Rep. 28. Univ. Saskatchewan. 101 p.

Willard, J.R. 1973d. Soil Invertebrates: VIII. A summary of populations and biomass. IBP Tech. Rep. 56. Univ. Saskatchewan. 110 p.

Wong, R. (per. comm.) Canadian Forest Service, 5320 - 122 Street, Edmonton 20, Alberta.

Zaika, V.E. 1973. Specific Production of Aquatic Invertebrates. Transl. E. Gollek. J. Wiley, New York. 154 p.

Zeuthen, E. 1953. Oxygen uptake as related to body size in organisms. Q. Rev. Biol. 28: 1-12.

Zinkler, D. 1970. Carbohydrasen Struebewohnender Collembolen und Oribatiden. p. 329-334. Colloquim Pedobiologiae. Dijon, Paris.

Appendix 1. *Gynaephora* feeding study at Truelove, 1972. Results are shown in grams dry weight and calories, converted from live weights. A. Conversion Factors. B. Food Offered. C. Consumption and Assimilation. D. Growth. E. Efficiencies

A: Conversion Factors

Controls	Fresh Wt.	Dry Wt.	cal/g Dry Wt.	Dry Wt./ Live Wt.	Conversion Factor, Wt.: Live/Dry	Conversion Factor, cal: $\bar{x}$ cal/g
Weighed, dried <i>Saxifraga oppositifolia</i> <i>Dryas integrifolia</i> <i>Salix arctica</i>	0.490 4.352 3.809	0.0911 1.6105 1.1642	4752 5056 4965	0.1859 0.3701 0.3056		
Weighed, put outside, dried <i>S. oppositifolia</i> <i>D. integrifolia</i> <i>S. arctica</i>	0.490 4.252 3.872	0.0979 1.6721 1.2147	4971 4878 5037	0.1998 0.3933 0.3137	0.1934 0.3817 0.3097	4862 4967 5001

B: Food Offered

Larva No.	<i>Salix pyraea</i> <i>oppositifolia</i> Fresh Wt.	<i>S. oppositifolia</i> Dry Wt.	<i>S. oppositifolia</i> cal	<i>Dryas</i> <i>integrifolia</i> Fresh Wt.	<i>D. integrifolia</i> Dry Wt.	<i>D. integrifolia</i> cal	<i>Salix arctica</i> Fresh Wt.	<i>S. arctica</i> Dry Wt.	<i>S. arctica</i> cal	Total Food Dry Wt.	Total Food cal
121	0.0	0.0	0.	0.218	0.0832	413.	2.643	0.8185	4094.	0.9017	4507.
120	0.0	0.0	0.	2.916	1.1130	5528.	0.0	0.0	0.	1.1130	5528.
190	0.0	0.0	0.	3.324	1.2688	6302.	0.0	0.0	0.	1.2688	6302.
189	0.0	0.0	0.	2.831	1.0806	5367.	0.0	0.0	0.	1.0806	5367.
118	0.0	0.0	0.	3.588	1.3695	6803.	0.0	0.0	0.	1.3695	6803.
196	0.0	0.0	0.	1.876	0.7161	3557.	0.0	0.0	0.	0.7161	3557.
27	0.476	0.0921	448.	0.519	0.1981	984.	1.788	0.5537	2769.	0.8439	4201.
63	0.278	0.0538	261.	0.446	0.1702	846.	2.774	0.8591	4296.	1.0831	5403.
64	0.252	0.0487	237.	0.424	0.1618	804.	2.167	0.6711	3356.	0.8917	4397.
145	0.0	0.0	0.	2.002	0.7642	3796.	0.0	0.0	0.	0.7642	3796.
146	0.0	0.0	0.	2.474	0.9443	4690.	0.0	0.0	0.	0.9443	4690.
57	0.287	0.0555	270.	1.030	0.3932	1953.	0.0	0.0	0.	0.4487	2223.
183	0.0	0.0	0.	0.0	0.0	0.	2.527	0.7826	3914.	0.7826	3914.
184	0.0	0.0	0.	0.0	0.0	0.	3.474	1.0759	5381.	1.0759	5381.
125	0.0	0.0	0.	0.234	0.0893	444.	2.974	0.9210	4606.	1.0104	5050.
127	0.0	0.0	0.	0.240	0.0916	455.	3.032	0.9390	4696.	1.0306	5151.
182	0.0	0.0	0.	2.531	0.9661	4799.	0.536	0.1660	830.	1.1321	5629.
139	0.0	0.0	0.	0.206	0.0786	391.	2.539	0.7863	3932.	0.8650	4323.
197	0.0	0.0	0.	1.917	0.7317	3634.	0.0	0.0	0.	0.7317	3634.
69	0.225	0.0435	212.	1.994	0.7611	3780.	0.230	0.0712	356.	0.8759	4348.
71	0.232	0.0449	218.	0.486	0.1855	921.	2.497	0.7733	3867.	1.0037	5007.
67	0.306	0.0592	288.	1.071	0.4088	2031.	0.0	0.0	0.	0.4680	2318.

Nos. 69 and 71 are hatching larvae, 20 individuals each No. initially
No. 67 is larva of *Bedena richardsoni* (Noctuidae)

C: Consumption and Assimilation

Larva No.	Food Uneaten Dry Wt.	Food Uneaten, cal/g	Food Uneaten, cal = (Fd. Uneat. Wt.)(cal/g)	Faeces Dry Wt.	Faeces cal/g	Faeces cal = (Faeces Wt.)(cal/g)	Consumption, Wt. = (Food Offered) - (Food Uneaten)	Assimilation, Wt. = (Consumption) - (Faeces)	Consumption, cal = (Fd. Offerd.) - (Fd. Uneat.)	Assimilation, cal = (Consumption) - (Faeces)
121	0.5782	5520.	3192.	0.1885	5211.	982.	0.3235	0.1350	1315.	333.
120	0.8267	5415.	4477.	0.2027	5414.	1097.	0.2863	0.0836	1052.	-46.
190	0.2876	5473.	1574.	0.6544	5052.	3306.	0.9812	0.3268	4728.	1422.
189	0.2363	5450.	1288.	0.4916	5358.	2634.	0.8443	0.3527	4079.	1445.
118	0.4696	5407.	2539.	0.6601	5148.	3398.	0.8999	0.2398	4263.	865.
196	0.2419	5528.	1337.	0.3954	5362.	2120.	0.4742	0.0788	2219.	99.
27	0.7043	5351.	3769.	0.2121	5189.	1101.	0.1396	-0.0725	432.	-668.
63	0.9098	5431.	4941.	0.1940	5175.	1004.	0.1733	-0.0207	462.	-542.
64	0.7776	5180.	4028.	0.0946	5604.	530.	0.1041	0.0095	369.	-161.
145	0.4359	5490.	2393.	0.1969	5285.	1041.	0.3283	0.1314	1403.	362.
146	0.3594	5362.	1927.	0.4415	5268.	2326.	0.5849	0.1434	2763.	438.
57	0.1633	5181.	846.	0.2429	5409.	1314.	0.2854	0.0425	1377.	63.
183	0.5303	5278.	2799.	0.1233	5089.	627.	0.2523	0.1290	1115.	487.
184	0.2580	5633.	1453.	0.4548	4886.	2222.	0.8179	0.3631	3927.	1705.
125	0.5852	5389.	3154.	0.2074	5149.	1068.	0.4252	0.2178	1896.	828.
127	0.5343	5543.	2962.	0.2123	5221.	1108.	0.4963	0.2840	2189.	1081.
182	0.3745	5338.	1999.	0.5773	5208.	3007.	0.7576	0.1803	3630.	623.
139	0.3433	5487.	1884.	0.3668	4953.	1817.	0.5217	0.1549	2439.	623.
197	0.6715	5426.	3644.	0.1853	5538.	1026.	0.0602	-0.1251	-9.	-1035.
69	0.7845	5531.	4339.	0.0204	6882.	140.	0.0914	0.0710	9.	-131.
71	1.0074	5288.	5327.	0.0278	4830.	134.	-0.0037	-0.0315	-320.	-454.
67	0.2539	5375.	1365.	0.0783	5726.	448.	0.2141	0.1358	954.	505.

D: Growth

Larva No.	Initial Wt. Live	Initial Wt. Dry	Final Wt. Live	Final Wt. Dry	% Wt. Increase = (Final Wt./Initial Wt.)	Growth, Dry Wt. = Final Wt. - Initial Wt.	Growth, cal = (Growth Wt.) (5668 cal/g)	Exuvium, est. Dry Wt.	Exuvium cal, est. = (Exuv. Wt.) (5458 cal/g)	Growth Total, Dry Wt. = (Growth + Exuvium)	Growth Total, cal = (Growth + Exuvium)
121	0.234000	0.050310	0.334000	0.071810	42.7	0.021500	121.9	0.0025	13.6450	0.0240	135.51
120	0.228000	0.049020	0.233000	0.050095	2.2	0.001075	6.1	0.0025	13.6450	0.0036	19.74
190	0.563000	0.121045	0.812000	0.174580	44.2	0.053535	303.4	0.0	0.0	0.0535	303.44
189	1.081000	0.232415	1.179000	0.253485	9.1	0.021070	119.4	0.0	0.0	0.0211	119.42
118	0.722000	0.155230	0.730000	0.156950	1.1	0.001720	9.7	0.0075	40.9350	0.0092	50.68
196	0.627000	0.134805	0.583000	0.125345	-7.0	-0.009460	-53.6	0.0065	35.4770	-0.0030	-18.14
27	0.231000	0.049665	0.221000	0.047515	-4.3	-0.002150	-12.2	0.0025	13.6450	0.0004	1.46
63	0.123000	0.026445	0.260000	0.055900	111.4	0.029455	167.0	0.0015	8.1870	0.0310	175.14
64	0.061000	0.013115	0.094000	0.020210	54.1	0.007095	40.2	0.0008	4.3664	0.0079	44.58
145	0.192000	0.041280	0.264000	0.056760	37.5	0.015480	87.7	0.0020	10.9160	0.0175	98.66
146	0.264000	0.056760	0.502000	0.107930	90.2	0.051170	290.0	0.0025	13.6450	0.0537	303.68
57	0.300000	0.064500	0.327000	0.070305	9.0	0.005805	32.9	0.0030	16.3740	0.0088	49.28
183	0.235000	0.050525	0.285000	0.061275	21.3	0.010750	60.9	0.0025	13.6450	0.0133	74.58
184	0.652000	0.140180	0.816000	0.175440	25.2	0.035260	199.9	0.0070	38.2060	0.0423	238.06
125	0.283000	0.060845	0.502000	0.107930	77.4	0.047085	266.9	0.0030	16.3740	0.0501	283.25
127	0.152000	0.032680	0.387000	0.083205	154.6	0.050525	286.4	0.0015	8.1870	0.0520	294.56
182	0.593000	0.127495	0.633000	0.136095	6.7	0.008600	48.7	0.0	0.0	0.0086	48.74
139	0.761000	0.163615	0.627000	0.134805	-17.6	-0.028810	-163.3	0.0	0.0	-0.0288	-163.29
197	1.184000	0.254560	0.946000	0.203390	-20.1	-0.051170	-290.0	0.0	0.0	-0.0512	-290.03
69	0.001100	0.000236	0.002500	0.000537	127.3	0.000301	1.7	0.0	0.0	0.0003	1.71
71	0.001200	0.000258	0.002800	0.000602	133.3	0.000344	1.9	0.0	0.0	0.0003	1.95
67	0.103000	0.022145	0.202000	0.043430	96.1	0.021285	120.6	0.0	0.0	0.0213	120.64

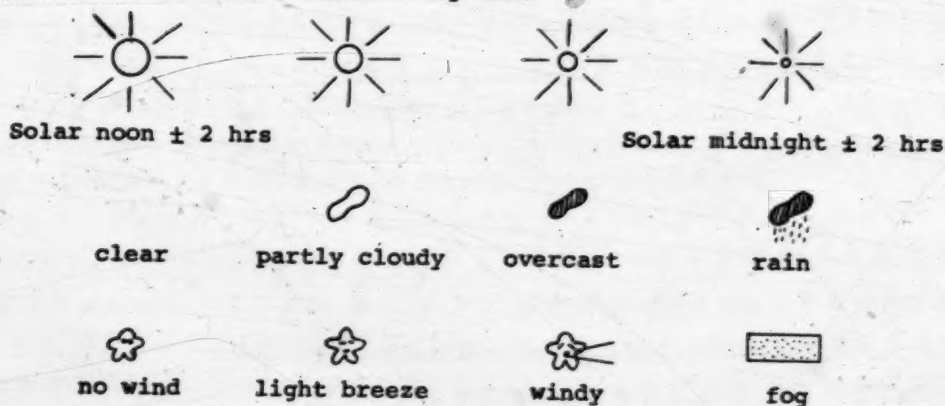
E: Efficiencies

Larva No.	Growth Efficiency, Gross, Wt. = (Growth/Consumption)	Growth Efficiency, Net, Wt. = (Growth/Assimilation)	Growth Efficiency, Gross, cal = (Growth/Consumption)	Growth Efficiency, Net, cal = (Growth/Assimilation)	Growth Efficiency, Total, Net, Wt. = (Growth/Assimilation)	Growth Efficiency, Total, Net, cal = (Growth/Assimilation)
121	6.645E-02	1.592E-01	9.266E-02	3.661E-01	1.777E-01	4.071E-01
120	3.754E-03	1.285E-02	5.793E-03	-1.338E-01	4.274E-02	-4.334E-01
190	5.456E-02	1.638E-01	6.418E-02	2.134E-01	1.638E-01	2.134E-01
189	2.496E-02	5.974E-02	2.927E-02	8.262E-02	5.974E-02	8.262E-02
118	1.911E-03	7.172E-03	2.287E-03	1.127E-02	3.844E-02	5.858E-02
196	-1.995E-02	-1.201E-01	-2.416E-02	-5.397E-01	-3.758E-02	-1.826E-01
27	-1.540E-02	2.966E-02	-2.820E-02	1.323E-02	-4.828E-03	-2.182E-03
63	1.700E-01	-1.424E+00	3.612E-01	-3.082E-01	-1.496E+00	-3.233E-01
64	6.816E-02	7.471E-01	1.089E-01	-2.498E-01	8.313E-01	-2.769E-01
145	4.716E-02	1.178E-01	6.256E-02	2.425E-01	1.331E-01	2.726E-01
146	8.748E-02	3.568E-01	1.050E-01	6.629E-01	3.742E-01	6.941E-01
57	2.034E-02	1.367E-01	2.390E-02	5.244E-01	2.074E-01	7.853E-01
183	4.261E-02	8.333E-02	5.465E-02	1.250E-01	1.027E-01	1.530E-01
184	4.311E-02	9.711E-02	5.089E-02	1.172E-01	1.164E-01	1.396E-01
125	1.107E-01	2.162E-01	1.407E-01	3.222E-01	2.300E-01	3.420E-01
127	1.018E-01	1.779E-01	1.308E-01	2.649E-01	1.832E-01	2.725E-01
182	1.135E-02	4.770E-02	1.343E-02	7.824E-02	4.770E-02	7.824E-02
139	-5.523E-02	-1.860E-01	-6.694E-02	-2.623E-01	-1.860E-01	-2.623E-01
197	-8.497E-01	4.091E-01	3.183E+01	2.801E-01	4.091E-01	2.801E-01
69	3.295E-03	4.242E-03	1.862E-01	-1.300E-02	4.242E-03	-1.300E-02
71	-9.287E-02	-1.092E-02	-6.089E-03	-4.290E-03	-1.092E-02	-4.290E-03
67	9.942E-02	1.568E-01	1.265E-01	2.388E-01	1.568E-01	2.388E-01

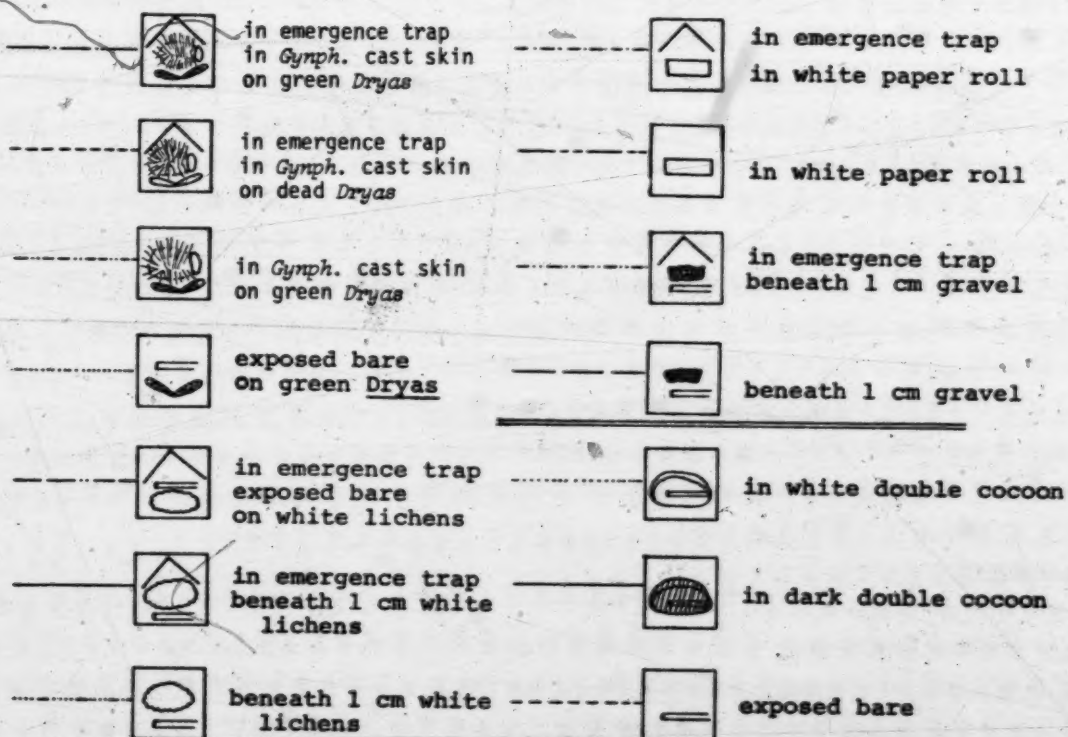
Appendix 2. Field temperatures recorded in and on assorted substrates, particularly *Gynaephora* larval exuviae and empty cocoons, compared to Stevenson Screen air temperatures, 1973. A. July 26. B. July 29, 27. C. July 30. D. Cocoons, August 1.

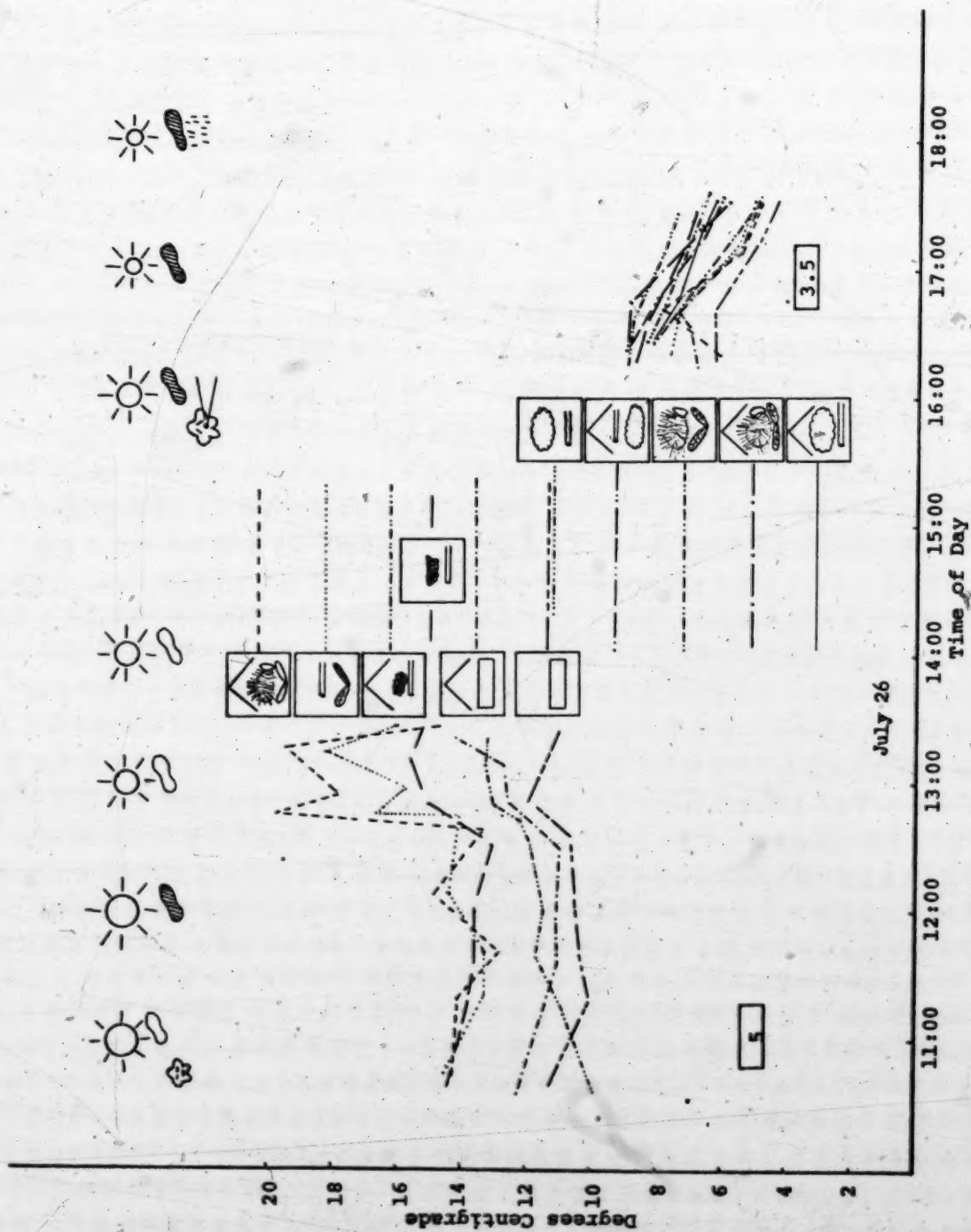
LEGEND FOR FIELD TEMPERATURE GRAPHS

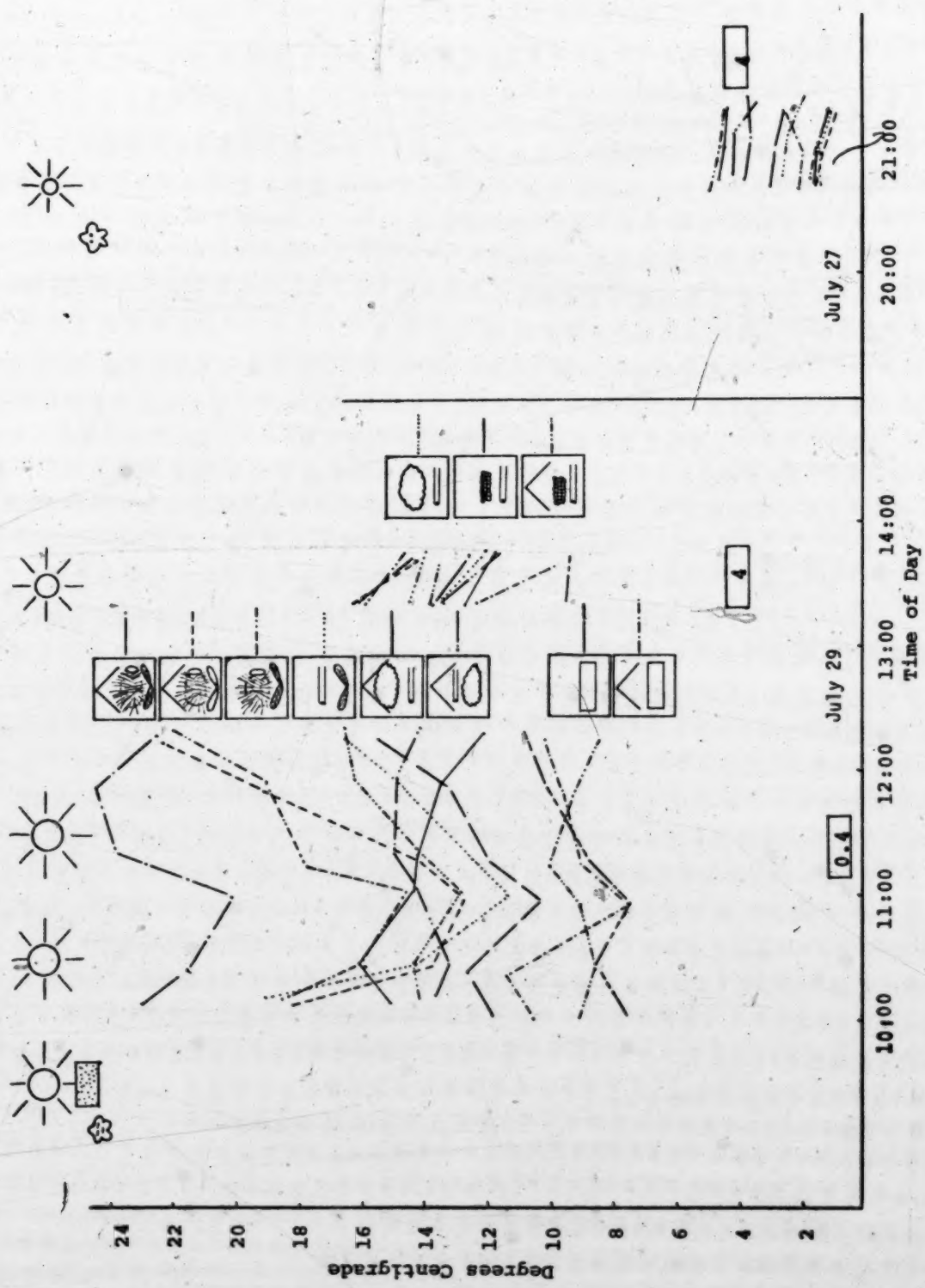
Weather Symbols



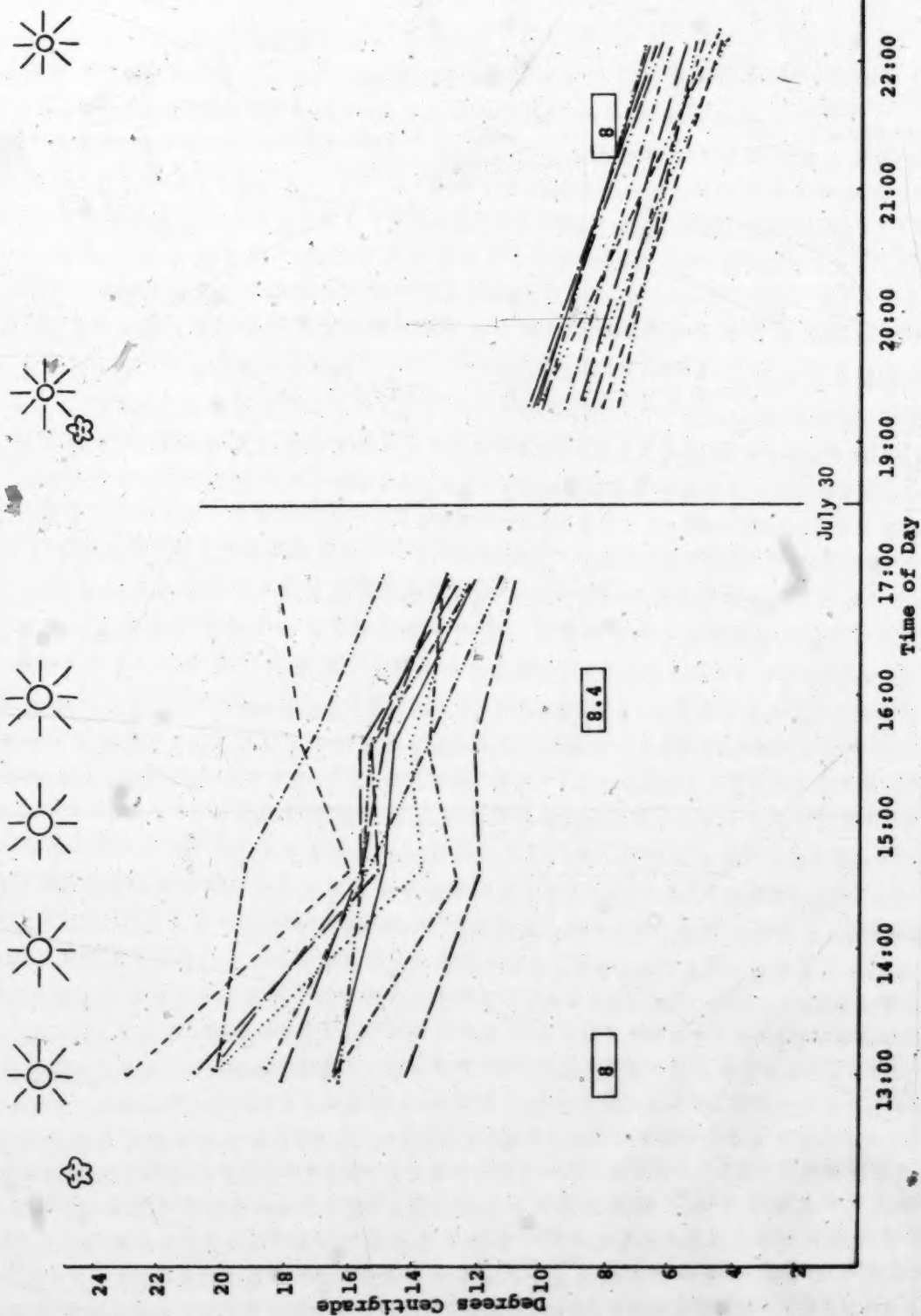
Thermocouple Symbols

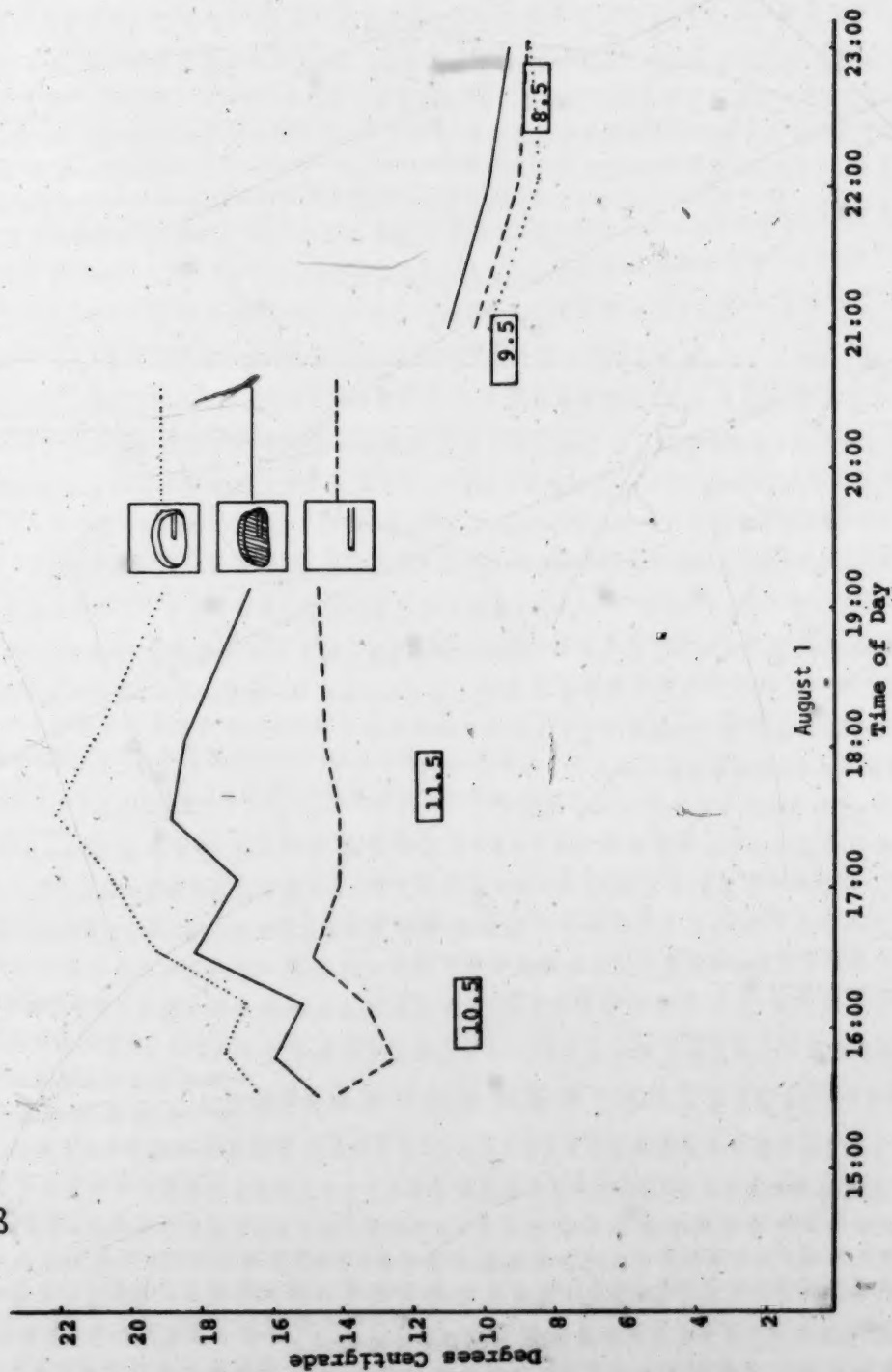




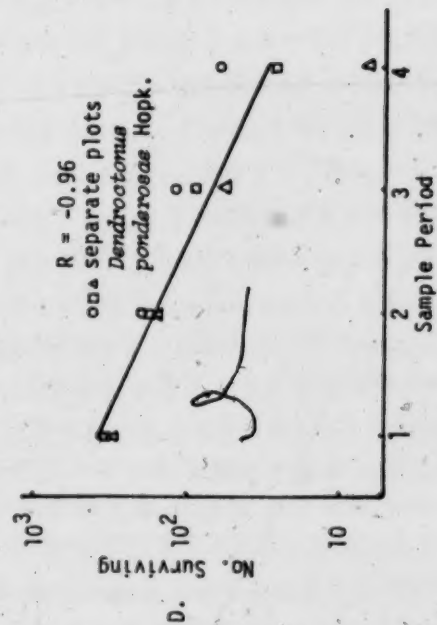
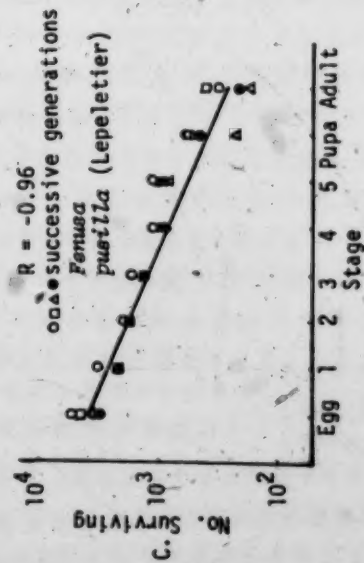
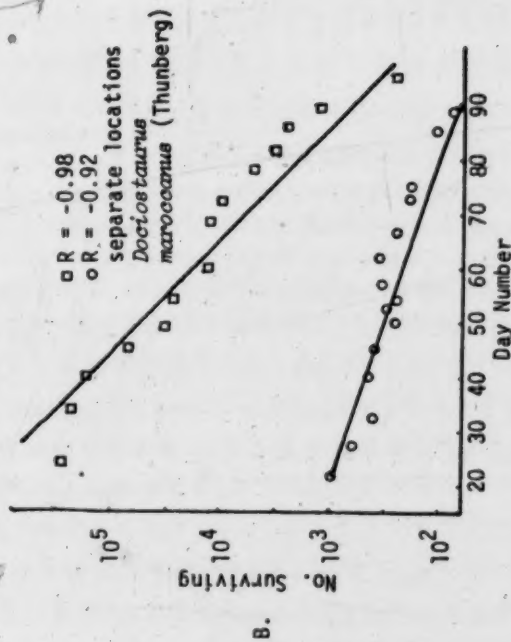
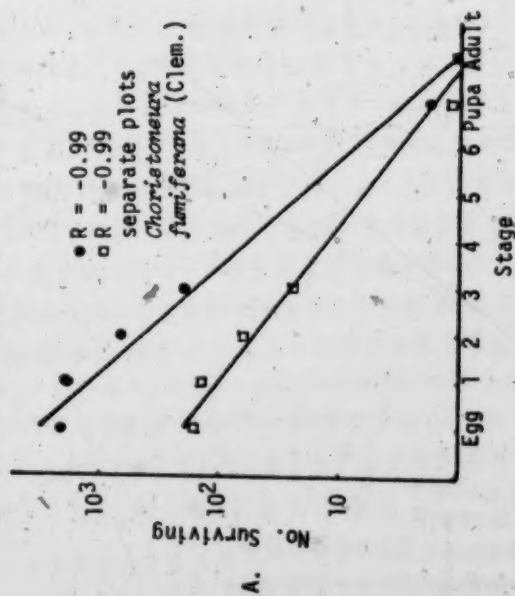


Appendix 2.8.

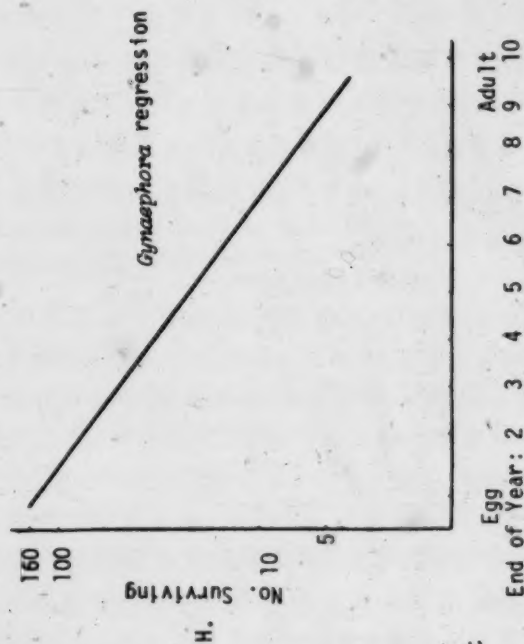
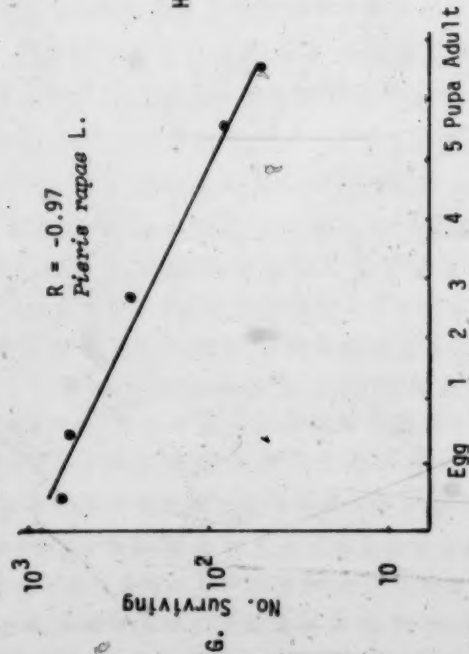
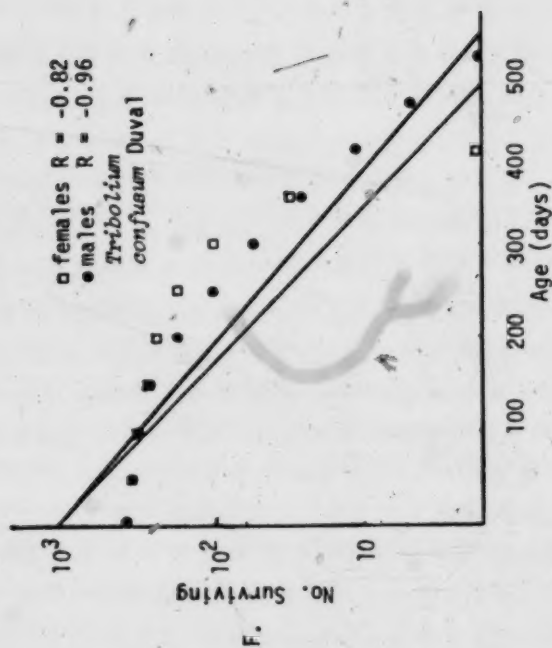
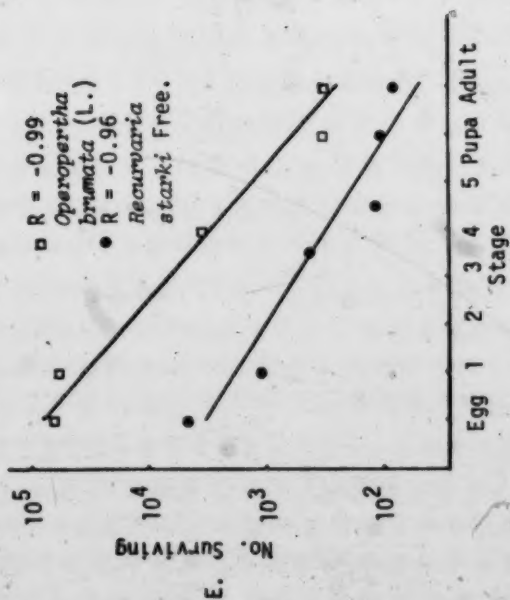




Appendix 3. Life table regression of survivors in a cohort against development. A. Morris & Miller (1954). B. Dempster (1956). C. Cheng & LeRoux (1966). D. Knight (1959). E. Embree (1965), Stark (1958). F. Pearl, Park, & Miner (1941). G. Harcourt (1966). H. Proposed *Gunaephora* survivorship.



Appendix 3 (con't)



Appendix 4. Program for computer portion of 12 C energy flow model.

This was run on a computer assembled by D.W.A. Whitfield.

Print and Input " $W_0, W_1, N_0, N_1, A, B, C, F$ in cal per mg"

Let $D = -\log(N_1/N_0)/\log(W_1/W_0)$

Print "Alpha/Beta ="; D

Let $P_1 = N_0 \times W_0^D \times (W_1^{(1-D)} - W_0^{(1-D)})/(1-D)$

Print "Production ="; P_1 ; "micrograms"

Let $P_2 = P_1 \times F/1000$

Print "Production ="; P_2 ; "calories"

Let $B_1 = N_0 \times A \times W_0^B \times ((W_1/W_0)^B \times N_1/N_0 - 1)/C/(B-D)/P_1$

Print "Beta ="; B_1 ; "hours to the minus one"

Let $T = \log(W_1/W_0)/B_1$

Print "T ="; T ; "hours"

Let $T_2 = T/2$

Print "T ="; T_2 ; "degree days"

Let $R = C \times P_1/1000$

Print "Respiration ="; R ; "microliters"

Let $R_1 = R \times 0.0047$

Print "Respiration ="; R_1 ; "calories"

Let $A_1 = D \times B_1$

Let $W = W_0 \times A_1 \times (W_1/W_0 \times N_1/N_0 - 1)/(B_1 - A_1)/(1 - N_1/N_0)$

End

Appendix 5. Summary of comparative soil core extractions: mean numbers, and biomass, m⁻²

A. Mean numbers m⁻²

Extraction Method	No. samples	Nematoda	Enchytraeidae	Tardigrada	Copepoda	Ostracoda	Acarina	Collembola	Tipulidae	larval Diptera	other Nematocera
Raised beach											
Tullgren fun.	7	-	-	-	-	-	3737	4191	-	-	-
Baermann fun.	8	30636	309	677	-	-	-	-	-	-	59
O'Connor fun.	6	34987	4653	1355	-	-	412	3652	-	-	177
Macfad. Hi-Gr.	4	59	707	-	-	-	6185	35654	-	-	707
Salt-Hollick*	8	353400	-	147	-	-	4231	28049	-	-	-
(Willard lab)		404290	-	-	-	-	10608	25282	-	-	-
Meadow											
Tullgren fun.	7	-	-	-	-	-	3685	1969	-	-	44
Baermann fun.	8	39529	839	1266	5434	574	-	44	-	-	4065
O'Connor fun.	6	82931	25268	1473	20556	412	884	236	59	-	11898
Macfad. Hi-Gr.	4	88	2297	-	1502	-	1414	1591	88	-	5474
Salt-Hollick	8	313378	-	-	-	-	1726	1471	-	-	441
(Willard lab)		893660	-	-	-	-	2917	1238	-	-	441

*Salt-Hollick samples were counted in Edmonton and Saskatoon (in Dr. Willard's laboratory). Figures are given for both counts. In Edmonton, Acarina were separated into those considered live during extractions versus cast skins. Live numbers are given in the table; total counts were: raised beach 9591, meadow 3315. Willard lab. figures are total counts.

Appendix 5 (con't) Summary of comparative soil core extractions: mean numbers, and biomass, m^{-2} B. Mean biomass m^{-2} , mg oven dry weight

Extraction Method	No. samples	Nematoda	Enchytraeidae	Acarina	Collembola	larval Diptera
Raised beach						
Tullgren fun.	7			17.3	31.3	
Baermann fun.	8	41.7	3.9			
O'Connor fun.	6	45.5	96.2	47.9	114.9	
Macfad. Hi-Gr.	4			79.8	46.8	
Salt-Hollick*	8	139.				
Meadow						
Tullgren fun.	7			23.6	14.9	
Baermann fun.	8	49.9	10.7			
O'Connor fun.	6	103.	506.	16.9	5.3	131
Macfad. Hi-Gr.	4			40.8	2.9	
Salt-Hollick	8	103.				

*Salt-Hollick weights are from Edmonton counts; Acarina are those considered "live" during extraction

Appendix 6. Emergence traps, 1972. Mean biomass of insects and spiders collected $m^{-2} yr^{-1}$ *

Location	All winged insects			Chironomidae & Sciaridae			Mescoidea		
	$\bar{x}$	s.d.	S.E.	$\bar{x}$	s.d.	S.E.	$\bar{x}$	s.d.	S.E.
ISSM	54.13	14.12	6.31	33.50	8.11	3.63	18.61	12.71	5.69
ISSRB	9.36	3.64	1.63	3.26	1.16	0.52	2.13	0.67	0.30
Besh	13.96	10.60	4.74	6.71	7.50	3.36	2.16	1.48	0.66
MesM	26.73	11.43	5.11	19.14	10.90	4.87	6.76	7.56	3.38
E.W.L.	20.44	11.30	5.05	11.85	6.06	2.71	5.29	6.31	2.82
S. & N.W.L.	21.33	8.13	3.64	12.78	5.84	2.61	8.17	4.80	2.15
HydM	50.51	30.81	13.78	33.16	11.68	5.22	16.52	21.66	9.69
all RB (7)	7.59	4.25	1.61	2.75	1.09	0.49	1.94	0.63	0.24
all M (28)	33.19	20.91	3.95	20.81	12.69	2.40	10.16	12.08	2.28
Tipuloidea			all Hymenoptera			only Tenthredinidae			
all	0.63	2.38	0.40	0.73	1.69	0.33	0.49	1.85	0.31
all RB	1.33	3.09	1.17						
all M	0.44	2.17	0.40						

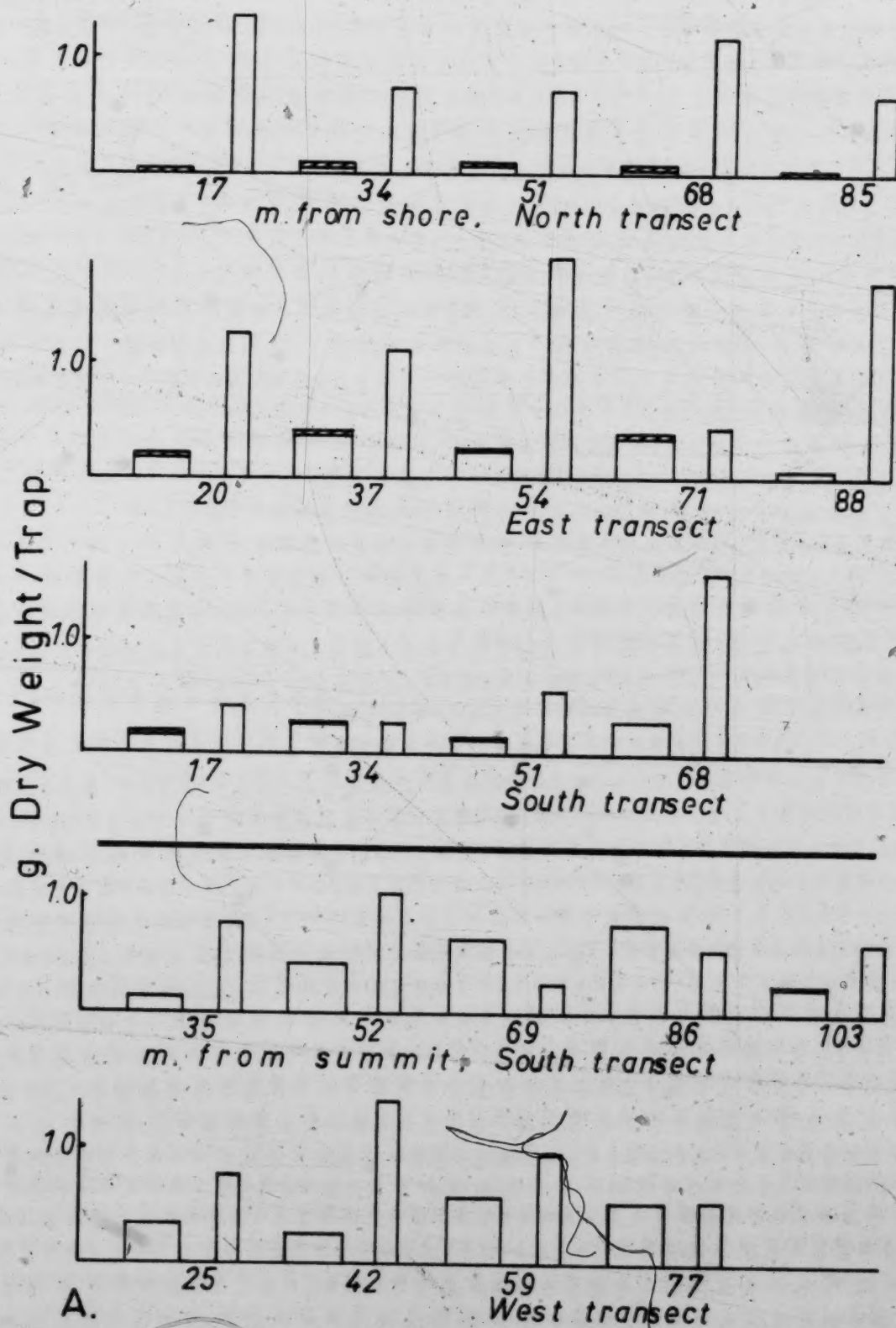
* Values are mg oven dry weight

Appendix 7. Pitfall trap results.

- A. Spiders and pterygote insects caught (per trap) along transects extending from the shore of Water Lake, and on land-locked Beschel Hill.

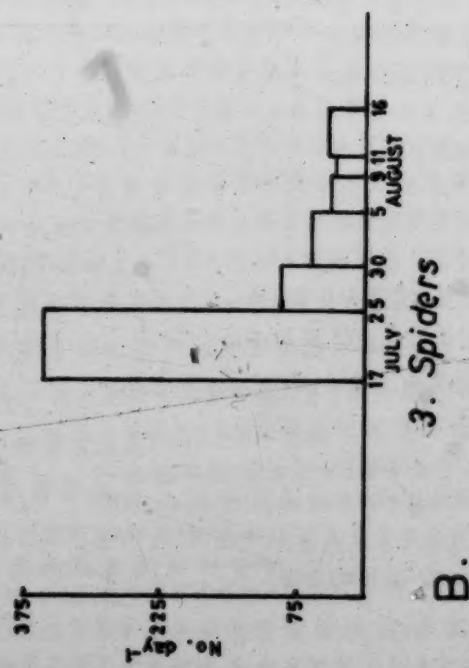
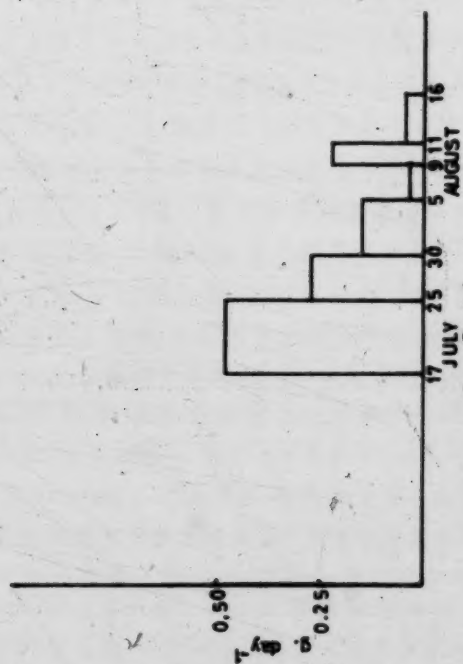


- B. Daily summaries. 1.2.3. Summary of these 1972 transect results (23 traps) as averages through the season. 4. Summary of 1971 spider catch (9 traps).



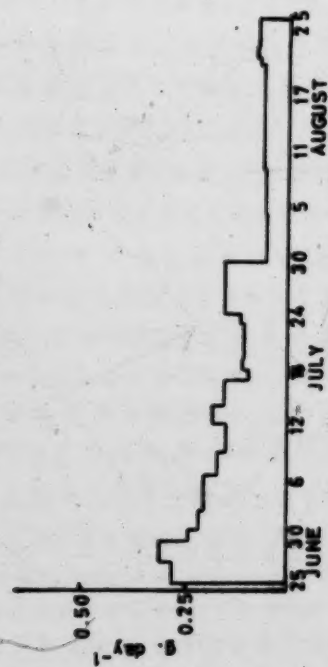


2. Spiders



B.

4. Spiders, 1971



Appendix 8. Inputs and calculations of the energy flow model. A. Inputs for the computer

Taxon	Site	µg Initial Wt.	µg Final Wt.	Initial No.	Final No.	"a" value ⁺	cal mg ⁻¹	"c" value
Rotifera	M	0.01	0.1	20	2	4.869	"	"
"	R b	"	"	"	"	"	"	"
Enchytraeidae	M	3.1	66.8	10	1.2	3.238	5.135	1092.6
"	R b	"	"	"	"	"	"	"
Tardigrada	M	0.1	1.6	24	3	"	5.8	617.2
"	R b	"	"	"	"	"	"	"
Crustacea								
Calanoidea-plus	M	0.2	40	100	4	4.869	5.35	569.1
Harpacticoidea	M	0.025	1.25	18	3	"	"	"
Acarina	M	0.23	6.9	60	6	0.5621	5.5	585.1
"	R b	0.33	9.9	"	"	"	"	"
Araneida								
Linyphiidae	M	10	750	16	3	(2,20)	5.8	1727.7
<i>Tarentula exasperans</i>	R b	450	45000	70	5	"	"	"
Collembola	M	0.59	16.52	60	8.7	1.447	"	617.2
"	R b	0.64	17.92	"	"	"	"	"
Lepidoptera	R b	19.37	5810	100	5	4.556	"	987.2
Diptera								
Chironomidae-plus	M	0.117	56.30	160	"	4.105	"	617.2
Mycetophilidae	M	1.031	495	"	"	"	"	"
Cyclorrhapha-plus	M	10.9	2179	80	"	1.622	"	"
Tipuloidea	R b	9.375	4500	160	"	4.105	"	"
Chironomidae-plus	R b	0.134	64.17	"	"	"	"	"
Cyclorrhapha-plus	R b	4.155	831	"	"	1.622	"	"
Hymenoptera								
Symphyta	M	4.65	1395	100	"	4.556	"	"
"	R b	15.30	4590	"	"	"	"	"
Apocrita	M	4.90	882	80	40	4.105	"	"
"	R b	5.08	915	"	"	"	"	"

⁺brackets indicate 10 C "a" value

Appendix 8. Inputs and calculations of the energy flow model. 8. Calculator inputs, and predictions about populations

Taxon	Site	N m ⁻² yr ⁻¹	Cohorts m ⁻²	Predicted		Joules R/P	Immatures	Lifespan
				ug mean Wt. /immature	ug mean Wt. population			
Protozoa	M			0.016			0.5	
Rotifera	M	6400	729.2	0.077	0.08	(0.05)	0.5	0.71
"	R b	220	25.07	"	"	"	"	"
Enchytraeidae	M	27500	6351	12.5	20.4	21.2	1.0	1.4
"	R b	9700	2240	"	"	20.7	"	"
Tardigrada	M	2300	209.1	0.33	0.47	(0.3)	0.5	0.66
"	R b	5760	523.6	"	"	"	"	"
Crustacea								
Calanoidea-plus	M	3488	111.2	2.26	4.27	(6.3)	"	0.74
Harpacticoida	M	20213	2068.8	0.19	0.34	(0.34)	"	2.23
Acarina	M	9690	779.6	1.07	3.99	4.09	"	2.17
"	R b	9800	788.4	1.54	5.72	5.80	"	2.18
Araneida								
Linyphiidae	M	1.8	0.403	102	113	597	1.4	1.46
<i>T. exasperans</i>	R b	0.3	0.021	3996	4429	17500	"	1.42
Collembola	M	8740	703.2	2.91	4.81	4.88	0.5	0.77
"	R b	18220	1465.8	3.16	5.22	5.31	"	"
		adults						
Lepidoptera	R b	0.2	0.05	216			0.8	1.5
Diptera								
Chironomidae-plus	M	892.6	223.15	2.17	9.12		0.5	1.04
Mycetophilidae	M	0.8	0.2	19.1			"	"
Cyclorhapha-plus	M	13.2	3.3	147	738		"	1.12
Tipuloidea	R b	0.6	0.15	173	6270		"	1.04
Cyclorhapha-plus	R b	76.2	19.05	2.5	31		"	"
Cyclorhapha-plus	R b	4.6	1.15	56	64		"	1.12
Hymenoptera								
Symphyta	M	0.8	0.2	75.8			0.8	1.5
"	R b	0.2	0.05	249			"	"
Apocrita	M	1.0	0.031	148			0.5	2.14
"	R b	0.6	0.019	154			"	2.15

*brackets indicate population subsample, or estimate

Appendix 8. Inputs and calculations of the energy flow model. C. Energy flow in cohorts

Taxon	Site	Moult Factor	1/T	Lifespan		Cohort Production		Cohort Respiration	
				Immature cohorts/season	maximum, total seasons*	μ_g Immatures	μ_g (Pupae +) Adults	μ_l Immatures	μ_l (Pupae +) Adults
Protozoa	M			10					
Rotifera	M	-	1.142	3.7	0.54	0.286	0.2	0.300	0.123
"	R b	-	"	7.3	0.27	"	"	"	"
Enchytraeidae	M	-	1.202	0.5	2.8	78.7	80.2	174	33.9
"	R b	-	"	1.0	1.4	"	"	"	"
Tardigrada	M	0.1	"	1.6	0.67	2.99	4.8	4.37	2.01
"	R b	"	"	3.2	0.52	"	"	"	"
Crustacea									
Calanoidea-plus	M	0.06	1.142	0.9	2	218	160	203	117
Harpacticoida	M	"	"	1.8	2	2.70	3.75	3.47	12.9
Acarina	M	"	1.196	0.2	55	49.2	41.4	50	180
"	R b	"	"	0.4	29	70.6	59.4	71.7	260
Araneida									
Linyphiidae	M	"	-	0.1	10	1370	2250	5900	638
<i>T. exasperans</i>	R b	"	-	0.1	9	255000	225000	783000	58000
Collembola	M	1.0	1.120	0.4	6.1	140	144	159	110
"	R b	"	"	0.8	3.1	151	156	173	119
Lepidoptera	M	0.06	0.801	0.3	3.0	31500	11300	56400	23000
Diptera									
Chironomidae-plus	M	"	1.103	0.6	1.8	353	109	370	223
Mycetophilidae	M	"	"	0.4	2.3	3710	960	3250	1958
Cyclorhapha-plus	M	"	1.597	0.2	4.4	11400	4130	13000	8520
Tipuloidea	R b	"	1.103	0.6	1.6	28200	8730	29500	17800
Chironomidae-plus	R b	"	"	1.1	0.9	403	124	421	254
Cyclorhapha-plus	R b	"	1.597	0.5	1.9	4350	1580	4950	3250
Hymenoptera									
Symphyla	M	"	0.801	0.2	5.0	7560	2710	13500	5520
"	R b	"	"	0.3	2.9	24900	8910	44500	18200
Apocrita	M	"	1.103	0.4	2.4	4950	15000	23400	29300
"	R b	"	"	0.8	1.2	5130	15600	24300	30700

*pterygote insect pupae and adults not included

Appendix 8. Inputs and calculations of the energy flow model.

D. Respiration times, and seasonal temperatures.

I. Values of T(ime) for immatures, from respiration "a" values of Procter (1977a). T = 1.0 at 12 C.

	Values of "a" at 12 C	At 7 C "T" changes by:	At 2 C "T" changes by:	Mean "T"
Enchytraeidae	3.238	1.089	0.406	0.832
Crustacea	4.869	1.059	0.569	0.876
Acarina	0.5621	0.720	0.787	0.836
Collembola	1.447	0.785	0.893	0.893
Chironomidae	4.105	1.117	0.603	0.907
Muscidae	1.622	0.673	0.206	0.626
Lepidoptera	4.556	1.628	1.120	1.249

II. Accumulated net positive degree days above 0 C, means of 1971-73 (data adapted from Courtin, unpubl.).

	150 cm	10 cm	2 cm	-1 cm	-2 cm	-5 cm
Meadow	273.4	309.3	314.8	312.5	276.1	202.9
Raised beach	379.3	424.3	500.0	624.4	586.6	598.0

VITAE

I was born on November 28, 1945, in San Francisco, California. Shortly afterwards, my family moved to Oregon and Washington State, then to Los Angeles, then to North Carolina, then to Baltimore Maryland. I started school there. Ted's turtle, which we found just down the hill from his house, was my first pet. We moved soon, and moved often. I remember especially the 2 schools I attended in Long Beach, California. The second school I attended from Komandorski Village, at Parks Air Force base, was a converted hospital ward, with 2 grades in each ward. At this time I had a series of snakes, lizards and birds for pets. We moved to Hawaii, where I attended a ridiculous excuse for a public school. The military Pearl Harbour Elementary and Radford Jr. High schools were rigorous in contrast. I amassed a respectably large collection of Hawaiian seeds, and sea shells, in my 2 year stay. Returning to California, I attended 2 more schools before high school. Thus, I attended 12 schools across the U.S. before settling down for 4 years at Encinal High School in Alameda, California. In this time I was a newspaperboy for 2½ years, and worked in a printing shop part-time for about one year.

Following high school, I went to the University of California at Berkeley, and received a B.Sc. in Entomology. To support myself, I worked as a lab helper at the Lawrence Radiation Laboratory, and at the agricultural U.C. Gill Tract. Later, I worked as a lab assistant in Nematology. Upon graduating, I attended the University of California at Riverside as a graduate student in Entomology,

supported by graduate research assistantships. I dropped out of a PhD program, in good academic standing, after 2½ years. I then went to the University of Alberta, where I have been enrolled for 7 years as a graduate student in Entomology. There I worked continuously on the research described herein. My support came through graduate research and teaching assistantships, teaching, and driving a taxi.